ECOLOGICAL PARADIGMS, SPECIES INTERACTIONS, AND PRIMARY SUCCESSION ON PHOSPHATE-MINED LAND

by

WILLIAM JAMES DUNN

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1989

ACKNOWLEDGMENTS

I thank my faculty committee members Dr. G. Ronnie Best, Dr. H. T. Odum, Dr. Clay Montague, Dr. Steve Humphrey, and Dr. Warren Vieseman for their guidance.

The research was supported by Florida Institute of Phosphate Research grant number 81-03-006, "Enhanced Ecological Succession Following Phosphate Mining," G. R. Best and H. T. Odum, principal investigators.

Several mining companies provided support and information. Marsh studies at Fort Green were in part supported by Agrico Mining Company. Mobil Chemical Company, International Minerals and Chemical Company, Gardinier Phosphate Company, and W. R. Grace and Company provided access to study sites.

Special thanks go to those who assisted with field work, Pete Wellece, Mel Rector, Alfonso Hernandez, Juan Hernandez, Bob Tighe, Jim Feiertag, and Tim King. The late Bill Coggins ran all the SAS analyses. Dr. Ron Myers allowed the use of unpublished data on sand banks at Lake Kanapaha.

Marla Mittan helped with technical editing. I wish to thank CH2M HILL for making its resources available during the final phases of this dissertation.

I sincerely thank my wife, Buffy, for her eternal patience and support during this degree. Finally, I thank my two sons Charlie and Sam for making life bearable during the "crunch."

TABLE OF CONTENTS

ACKNOWLEDGMENTS.....ii

ABSTRACT.....vi

INTRODUCTION.....1

Previous Studies of Succession on Mined Land.....2
Background and Concepts.....3
Succession Theory.....3
Wetland Succession.....9
Role of Consumers.....13
Competing Paradigms of Succession.....20
Initial Floristics.....20
Inhibition.....20
Relay Floristics.....24
Coevolution.....24
Self-organization.....24
Changes in Paradigms.....24
Hypotheses and Objectives.....27
Marsh Development.....28
Upland Forest Development.....29
Mound-building Ants and Ecosystem Development.....30
Description of Study Sites.....33

METHODS.....43

Marsh Development.....43
Seed Bank Survey.....43
Marsh Transect Study.....45
Upland Forest Studies.....47
Direct-seeded Plots.....50
Seedling Transplant Plots.....51
Mound-building Ants and Upland Succession.....53
Survey of Mound Density.....53
Physical Soil Analyses.....53
Chemical Soil Analyses.....55
Plant Growth Study.....57
Statistical Analysis.....58

RESULTS....59

Marsh Development....59
Seed Bank Survey....59
Marsh Transect Study....72
Upland Forest Succession Plots....90
Seed Germination and Survival....90
Height Growth in Seed Plots....105
Height Growth in Transplant Plots....112
Mound-building Ants....114
Mound Survey....114
Plant Growth Study....114
Chemical Soil Analyses....116
Physical Soil Analyses....120

DISCUSSION....124

Marsh Development....124
Seed Bank Formation....124
Formation and Stability of Macrophyte Communities....126
Wetland Succession Model....132
Role of Life History Characteristics....132
Importance of Allogenic and Autogenic Factors....132
Eclectic Wetland Succession Paradigm....135
Upland Forest Succession Plots....139
Seed Germination and Survival....139
Height Growth....146
Species Removal....150
Competition....153
Succession....155
Caveats....157
Mound-Building Ants....158
Mound Survey....158
Ant Mound Roles....159
Ant Model....166
Eclectic Synthesis of Paradigms and Implications for Reclamation Design....168
Inhibition....170
Initial Floristics....172
Relay Floristics....174
Coevolution....174
Self-organization....176

CONCLUSIONS....179

REFERENCES....182

BIOGRAPHICAL SKETCH....193

Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

ECOLOGICAL PARADIGMS, SPECIES INTERACTIONS, AND PRIMARY SUCCESSION ON PHOSPHATE-MINED LANDS

By

WILLIAM JAMES DUNN

May 1989

Chairman: Dr. G. Ronnie Best
Major Department: Environmental Engineering Sciences

Field studies on phosphate-mined lands were undertaken to evaluate several paradigms for explaining succession, including inhibition, initial floristics, relay floristics, coevolution, and self-organization. Primary objects of study were wetland seed bank formation, formation and stability of wetland macrophyte communities, interactions between colonizing species and trees on upland sites, and the role of mound-building ants in upland succession.

A survey of natural and post-mining wetlands showed seed banks develop rapidly, but contain only wind-dispersed early successional species. Late successional marsh species can be added as an instant seed bank through muck material from a donor or, in some cases, by planting.

The development of a reclaimed marsh was monitored over its first four growing seasons. Results showed that while very different plant communities developed with the application of muck from a donor marsh as compared to natural succession, both types of initially established macrophyte communities remained stable throughout the monitored period.

Upland succession was enhanced with direct seeding and seedling transplants in four treatments: natural colonization, enhancement of natural colonizers, enhancement with legumes, and weeding. Tree seedlings had better height growth in plots in which the colonizing weeds were removed. Tests indicated that the five paradigms investigated operated concurrently during primary succession.

Fire ants (Solenopsis invicta) were the most commonly observed invertebrate species on mined lands, with well established populations within the first year after mining. Mound densities on 1- to 5-year old sites ranged from 560 to 2,000 per hectare. Mound soils had higher concentrations of sodium, potassium, total nitrogen, and organic matter than the adjacent non-mound soils. In greenhouse experiments, a grass and a woody plant exhibited enhanced growth on mound soils. Water infiltration rates were 5 to 100 times greater on mound soils than non-mound soils.

The view of the competing paradigms as mutually exclusive was not supported. A unifying paradigm may be possible from a more eclectic synthesis of the inhibition, initial

floriatica, relay floriatica, coevolution, and self-organization models.

INTRODUCTION

The pattern and process of ecosystem development, usually called succession, are a main focus of the science of ecology. The paradigms used to understand succession are still in controversy, and the pattern and process of ecosystem development are still much debated. A clear understanding of succession provides an opportunity for forming rational and cost-effective land reclamation techniques and policies that will enhance the successional process on disturbed lands. It is not possible to predict the long-term development of created and restored ecosystems without a clear understanding of the natural processes of ecosystem development. Unfortunately, the ecological literature remains divided on the fundamentals of succession, especially the interactions between early colonizing plant species and late successional species and the role of non-trophic interactions between producers and consumers.

The establishment of vegetation is one of the first stages of primary succesion on an abiotic substrate, whether the succession results from geologic uplift, glacial retreat, volcanic lava flow, landslide, or strip-mining. The post-mining landscape is a relatively simple ecosystem of few

species but provides a rich environment for testing paradigms describing the pattern and process of succession. Detailed ecological studies of the recovery process on mined lands may also identify some solutions to existing reclamation problems. The succession and human-managed reclamation of phosphate-mined lands in central Florida provides and opportunity to evaluate successional theory and use the knowledge to facilitate reclamation. This discussion examines successional processes on phosphate-mined lands, especially marsh development, upland forest development, and the roles played by sand banks and mound-building ants.

In a few cases an understanding of wetland succession has been translated into a successful technique for wetland creation and restoration. In the Tampa Bay area it was observed that formerly unvegetated intertidal areas were quickly colonized and stabilized by smooth cordgrass (Spartina alterniflora) which presumably helped mangrove seedlings to become established years later (Lewis 1982). In 15 to 20 years the mangroves eventually shaded out the cordgrass and became dominant. Lewis developed a technique for establishing a nurse crop of cordgrass which has since become a common practice for mangrove establishment.

Previous Studies of Succession on Mined Lands

Many studies of unreclaimed mined lands have documented the paucity of late successional species on upland sites

(Humphrey et al., 1978; Schnoes and Humphrey, 1987; Wallace, 1988) and wetland sites (Clewell, 1981; Rushton, 1983, 1988). Vegetation studies of phosphate clay settling ponds reported an initial cover of cattails (Typha sp.) and water hyacinths (Eichhornia crassipes) followed by primrose-willow (Ludwigia peruviana) and willow (Salix caroliniana). Wax-myrtle (Myrica cerifera) and vines dominated sites as they continued to dry (Zellars-Williams and Conservation Consultants, 1980; King et al. 1980; Rushton, 1983). These studies generally describe an arrested succession in which the initial species composition of primary invading species is perpetuated. In contrast, other studies (Kangas 1979, 1983) have described older sites where succession did not appear to be arrested or inhibited. In cases with a nearby seed source, sites were invaded by hardwood species such as red maple (Acer rubrum), laurel oak (Quercus laurifolia), and live oak (Quercus virginiana) (Zellars-Williams and Conservation Consultants, 1980; Rushton, 1983).

Background and Concepts

Succession Theory

Clements (1916) described succession as a universal, orderly process of progressive change. He asserted that the community developed from diverse pioneer stages to converge on a single, stable, mesophytic community (monoclimax) under

the control of the regional climate. He held that in succession, the community repeated a sequence of stages, similar to the development of an individual organism from birth through death, that was an orderly directional process predictable in its development. As succession proceeded, the community increasingly controlled its own environment and, barring disturbance, became a self-perpetuating climax. Succession occurred as waves of plant populations made conditions suitable, or "prepared the way," for the next wave and often to the detriment of their own continued survival.

To other ecologists of the time, the plant community was less well defined and succession less orderly, directional, and predictable than Clements suggested. Alternative concepts of succession voiced by Gleason (1917, 1926, 1939) advocated an individualistic, population-based approach in which the plant association is seen as a coincidence rather than an interdependent entity. The distribution of a particular species in the landscape depends on its migration characteristics and environmental requirements, and the plant community is an artifact solely dependent on the grouping of species with overlapping environmental requirements. Given sufficient time, all species had equal access to all sites, but species were found only on those sites with the appropriate environmental conditions. According to this allogenic theory, a particular species grows in the company of any other species with similar requirements and eventually

disappears from areas where environmental conditions are no longer favorable.

Egler (1954) also found fault with Clements' view of succession, but stressed the role of autogenic processes in old-field community succession. He applied the name "relay floristics" to Clements' sequential appearance and disappearance of groups of species and posed an alternative mechanism he termed "initial floristics" in which old-field plant community development after abandonment unfolds from an initial flora already residing within the soil, without additional increments by further invasion. As each successive species or group subside, another that has been present from the beginning, assumes dominance. In a forest succession sequence, eventually only the trees are left. Egler noted that the actual development of vegetation in an old-field is a function of both autogenic processes but that in secondary succession, initial floristics determined the composition of the resulting community and relay floristics played a relatively minor role. He also noted that allogenic factors were important determinants of community composition.

The Clementsian and Gleasonian views of succession define opposite poles within the field of ecology. In the modern analogs, the arguments have been refined but many of the key issues and differences have remained intact. The Clementsian tradition has a modern synthesis in systems ecology, while the modern proponents of the Gleasonian view are typically aligned

with the disciplins of population ecology. Dichotomies still center on questions of holism versus reductionism, the evolutionary unity of communities, and whether ecosystems possess emergent properties.

E.P. Odum (1969) provided a modern ecosystem reformulation of Clementsian succession. Odum noted the similarity of succession to the development of individual organisms and converged with Clements' description of succession as an orderly process that is reasonably directional and therefore predictable, resulting from modification of the physical environment by the community (autogenic) and culminating in a stabilized (climax, mature) ecosystem with homeostatic properties.

Confusion developed when some ecologists described the ecosystem as having an evolutionary unity. Patten (1975) called the ecosystem a "coevolutionary unit." Webster et al. (1974) stated that a basic assumption of ecosystem analysis is that ecosystems are units of selection and evolve from systems of lower selective value to ones of higher selective value that optimize utilization of essential resources. Other ecologists did not view communities or ecosystems as evolutionary units because inheritance of genes is passed separately by the many species.

H.T. Odum (1983) describes succession as a self-organizing process by which ecosystems develop structure and processes from the available choices supplied by seeding. The

organization develops new programs for succession with which species prevail that are reinforced by controls and material cycles of the next larger system. This view has maximum power as a self-design principle, in that there is survival of those combinations of components that contribute most to the collective power of the system. Species combinations are reinforced that divide up and optimize the use of resources to collectively maximize productivity, and species substitutions occur through time as new choices are offered and selected. Some Darwinian selfish selection is involved but is regarded as secondary. Emphasis is on selection of relationships that make the system perform, with evolution ultimately occurring but on a longer time interval.

Modern proponents of the Gleasonian individualistic view (McCormick, 1968, Drury and Nisbet, 1971, 1973; Horn 1971, 1974, 1975; Pickett, 1976; Connell and Slatyer, 1977) find the classical Clementsian paradigm and its modern incarnation, the holistic-ecosystem representation, unpalatable. McIntosh (1982) points out that the studies by these researchers share at least three characteristics:

1. They are commonly cited in recent discussion of succession as providing "new" insights for successional theory.

2. They are explicitly critical of Clements' holistic, organism theory of succession and of what they interpret as the successional theory of the organismic, holistic, ecosystem ecology expressed by ecosystem ecologists.

3. The alternative models of succession proposed advocate an individualistic, population-based approach emphasizing life history attributes of organisms and the consequence

of natural selection as the essential basis of a modern theory of succession.

Connell and Slatyer (1977) described three models by which species may replace each other in a successional sequence. They assumed no further changes in the abiotic environment and that certain species usually appear first because they have the ability to produce large numbers of easily dispersed seeds, which are not adapted to germinating and growing on occupied sites.

Model 1 assumes only certain early successional species are able to colonize a site immediately after disturbance, as in the "relay floristics" model of Egler and the classical Clementsian view.

Models 2 and 3 assume that any arriving species may be able to colonize, even those that typically appear late in the sequence. These are alternative forms of Egler's "initial floristics" model. In model 2, early colonists neither increase nor reduce the rates of recruitment and growth of later successional species. Species that "appear" later in the successional sequence are those that arrived either initially or later but grew very slowly. In Connell and Slatyer's model of initial floristics, the sequence of species is determined solely by life history characteristics. In contrast, model 3 (termed inhibition) holds that once early colonists secure the available space and resources, they inhibit invasion by subsequent species and suppress the growth

of these already present. Invasion is only possible when the dominating species are damaged or killed, thus releasing resources. In model 3, the tolerance of late successional species is important, as it allows them to survive long periods of suppression.

Wetland Succession

Much of the debate on succession focuses on the factors controlling the course of community development. Controlling factors are typically grouped as autogenic, those generated by the biological community itself, or allogenic, coming from outside the biological community.

In some views of succession (Clements, 1916, 1920) wetlands were considered a transient stage between aquatic communities and a terrestrial forest climax. In this concept, aquatic areas may gradually fill from sediment deposition and organic peat formation. Emergent macrophytes, shrubs, and trees gradually appear, and the community continues to transform the wetland site into a terrestrial one. Where sediment accumulation raises the ground elevation above water levels, a change to drier vegetation is observed.

In wetlands where inorganic sediments are not being added and land is not being elevated, peat formation may not proceed beyond water levels (Odum, 1984). In warm climates, organic matter oxidizes or burns in dry weather, arresting succession. Many wetland ecosystems in this sense are a form of climax

A major influence of Clements' ideas on wetland ecology was the tendency to interpret zonation patterns in wetlands as indicators of future successional trends. Succession in wetlands was viewed as a directional, autogenically-driven process leading inevitably to some terrestrial climax. Evidence leads to the conclusion that both allogenic and autogenic processes act to change wetland vegetation and that the Clementsian idea of a regional terrestrial climax for wetlands is often inappropriate.

Van der Valk (1981) claims that Pearsall (1920) was one of the first to apply Clements' concept of succession to wetlands. The concept of the monoclimax was eventually replaced by Whittaker's concept of pattern climax (Whittaker, 1953), which was based on gradient analysis studies that documented the independent distribution of species along environmental gradients. The effect was to de-emphasize the successional interpretation of zones, or vegetative zones in the case of wetlands, and to focus on the correlation of plant species with specific types of environmental conditions.

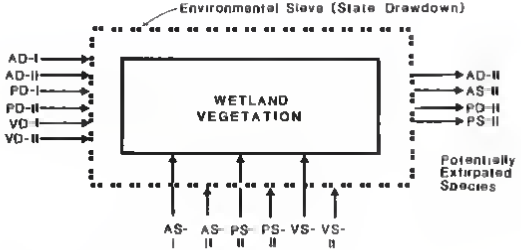
Van der Valk (1981) proposed a "new" definition of wetland succession, based on the ideas of H.A. Gleason (1917, 1925, 1939), that did not presuppose the existence of a climax vegetation. Van der Valk defined succession as a change in the floristic composition of the vegetation of an area from one year to another which, is narrower than Gleason's definition of it as any change, quantitative or qualitative,

in the vegetative cover of an area. In the van der Valk model, succession occurs whenever a new species becomes established or an existing one is extirpated.

The model is based on the life history characteristics of the wetland species and the interaction of the species with the prevailing environmental conditions (see Figure 1). Van der Valk classified wetland plant species into 12 life history strategies based on potential life span, propagule longevity, and propagule establishment requirements. Under this scheme, each life history type has its own unique set of characteristics and associated responses to prevailing environmental conditions, which act as a "sieve" in determining the species composition of the wetland. As environmental conditions change, so does the action of the sieve and, therefore, the species present.

The van der Valk model focuses on the wetland seed bank as the key biological component. The functional significance of seed banks lies in providing the plant community with an *in situ* means of regenerating from naturally occurring disturbances (Grime, 1978). Van der Valk (1981) and van der Valk and Davis (1976, 1978) have aptly documented and demonstrated the role seed banks play in the vegetation dynamics of prairie glacial marshes that undergo cyclic patterns of flooding-drawdown-drought. In prairie glacial marshes and other marsh systems (Keddy and Reznicek, 1982,

Figure 1. General model of Glaciation wetland succession proposed by Van der Valk (Source: after Van der Valk 1981)



KEY

A-Annual
P-Perennial with Limited Life Span
V-Vegetatively Progated Perennial
D Dispersal Dependent Species - Short-Lived Seeds
S-Seed Bank Species - Long Lived Seeds
I Species Established Only in Absence of Standing Water
II Species That Can Be Established In Standing Water

Leck and Graveline, 1979), seeds remain dormant, yet viable, in the seed bank during periods in which environmental conditions are unfavorable for germination, growth, and development of the population. In wetland and upland communities, seed banks provide a mechanism for rapid recovery from catastrophic mortality resulting from fire (Johnson, 1975), clear-cutting (Marks, 1974), and drought (Myers, 1983). Marks (1974) has shown that the rapid response of pin cherry to clear-cutting in the Hubbard Brook ecosystem helped minimize the effect of canopy removal on nutrient losses from the ecosystem. Egler's initial floristic hypothesis portrays old-field succession as a seed bank response.

The van der Valk wetland model can be reformulated using energy circuit language (Figure 2). Van der Valk's 12 life history categories are simplified to mudflat annuals, emergent macrophytes, and aquatic macrophytes. The actual composition of the wetland is determined by the interaction between the existing plant community, the propagules present, and environmental conditions. Logic switches are used to indicate the actions of the "environmental sieve."

Role of Consumers

Various roles are attributed to consumers in ecosystems beyond simple trophic relationships of herbivory and predation. These non-trophic interactions typically involve

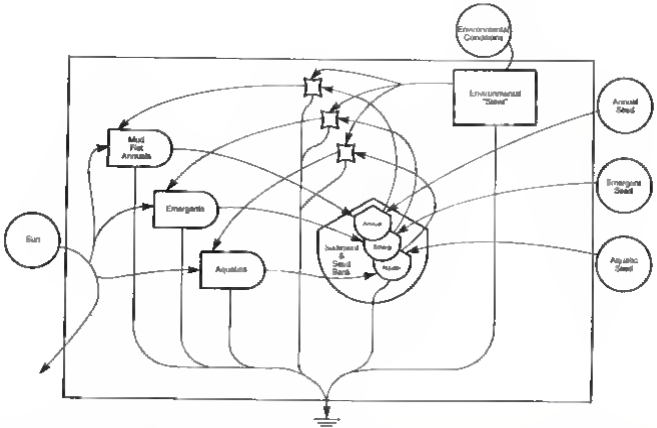


Figure 2. An energy circuit diagram of a Glasaonian model of wetland succession (redrawn from Van der Valk 1981)

hypothesized feedback loops between species, termed indirect effects. Non-trophic interactions are concerned with ecosystem structure and function, which, according to the individual selection theories of traditional population ecology, are not subject to adaptive evolution.

It has been suggested that heterotrophs regulate autotrophs and thereby control the rate of energy production (O'Neil et al., 1975; Lee and Inman, 1975). Owen and Weigert (1976) asked the question, whether consumers maximize plant fitness, and developed a hypothesis that consumers, like pollinators, have a mutualistic relationship with plants. They suggested that plants may exploit consumers to increase fitness. If, through the action of consumers, a nutrient that is in short supply is made more available to the plant, the relatively small amount of photosynthate lost may be more than compensated.

Mutualistic interactions may involve a direct trophic link, such as those just described, but other non-trophic interactions between species very much affect fitness but do not involve competition or predation. For example, intensive fiddler crab (Uca pugnax) activity in the tall-form of saltmarsh cordgrass (Spartina alterniflora) stands improves soil drainage, oxygenates marsh sediments, and increases belowground decomposition of plant-generated debris (Bertness, 1985), all of which can affect the growth rate of the cordgrass.

Population ecologists view non-trophic interactions as byproducts of the evolutionary process. Wilson (1980) described the problem as one in which traditional investigators within the disciplins of population ecology assumed that the community structure was already in place They then focused on relatively superficial forms of competition and predation, while ignoring the structure that actually determined the parameter values of the models.

Productivity in ecosystems depends on recycling and conservation of nutrient resources. The actions of consumers may cause a nutrient in short supply to become relatively more available. When primary production is nutrient-limited, heterotrophic activity, which accelerates mineralization, may help increase it. The importance of heterotrophs as regulators of ecosystem processes far outweighs their importance as measured by calories or grams of matter, but rather lies in how their characteristics affect or regulate ecosystem processes (Chew, 1974; Odum, 1982).

Numerous examples can be found of the regulatory role played by consumers. Vertebrate herbivores have been shown to increase productivity of grasslands (McNaughton, 1975). Platt (1975) showed the influence that badger mounds have on soil properties and the pattern and distribution of some plant species. Burrowing rodents can act as nutrient pumps, bringing materials to the surface from below (Abaturov, 1972). In forest soils, litter accumulated and decomposition slowed

when earthworms were removed (Witkamp, 1971). Earthworms stimulated the growth of potted barley seedlings, possibly by increases in vitamin B_{12} (Atlavinyte and Daciulyte, 1969). Dung beetle activity was found to be almost as effective as mechanical mixing in enabling plants to benefit from the nutrient storages in dung (Bornemissza and Williams, 1970). Leaf cutter ants (genus Atta) reduced primary productivity by reducing leaf area, but more than made up for that loss by returning materials to the soil (Lugo et al., 1973).

Mound-building ants can produce localized concentrations of organic matter and nutrients, resulting in changes in densities of bacteria, fungi, and plants (Czerwinski et al., 1971). They can affect the physical and chemical aspects of soil as well as the distribution of plants, bacteria, and fungi, and are important in making channels and burrows. Hopp and Slater (1948) felt ants could be as effective as earthworms in creating conditions for improved plant growth, while Thorpe (1949) indicated that ants may produce greater effects than earthworms. Shrikhande and Pathak (1949) reported that ants increased the organic matter content of soils second only to earthworms.

Numerous studies have shown chemical differences between mound and nearby non-mound soils, with evidence of higher levels of exchangeable cations, micronutrients, nitrogen, phosphorus, and organic matter, as well as differences in pH and conductivity (Czerwinski et al., 1969, 1971; Gentry and

Stiritz, 1972; Rogers and Lavigne, 1974; Wali and Kannowski, 1975; King, 1977; Petal, 1979; Levan and Stone, 1993; Culver and Beattie, 1993). Enhanced nutrient levels in mound soils are attributed to microbially-mediated mineralization of organic waste products in the mound (Petal, 1979). This is supported by the work of Czerwinski et al. (1971), who showed the abundance of bacteria and fungi in ant mounds is higher than in the surrounding soil.

Mound-building ants profoundly alter the soil profile characteristics at their nest sites (Baxter and Hole, 1967; Salem and Hole, 1968; Wilkes et al., 1976; Wali and Kannowski, 1975; Alvarado et al., 1981; Levan and Stone, 1993). Mound soil has been shown to differ from nearby soil in bulk density, porosity, and infiltration capacity (Rogers and Lavigne, 1974; Rogers, 1972; Wali and Kannowski, 1975).

Through their influence on soils, ants can affect microtopographic heterogeneity, which can influence species composition, standing crop, and successional status of the local vegetation (Petal, 1979; Rogers, 1974; Gentry and Stiritz, 1974; King, 1977; Culver and Beattie, 1993). Herbs flourish on abandoned nest sites of harvester ants (Gentry and Stirita, 1972) and are known to affect seed distribution. Ants are known to alter sand shadows in deserts (Bullock, 1974; O'Dowd and Hay, 1990), mesic environments (Beattie and Lyons, 1975; Handel, 1997; Beattie and Culver, 1991), and tropical forests (Roberts and Heithaus, 1986). Some plant

species known as myrmecochorse have a food body on their seed that is eaten by ants, which then disperes the seeds while returning food materials to the mound.

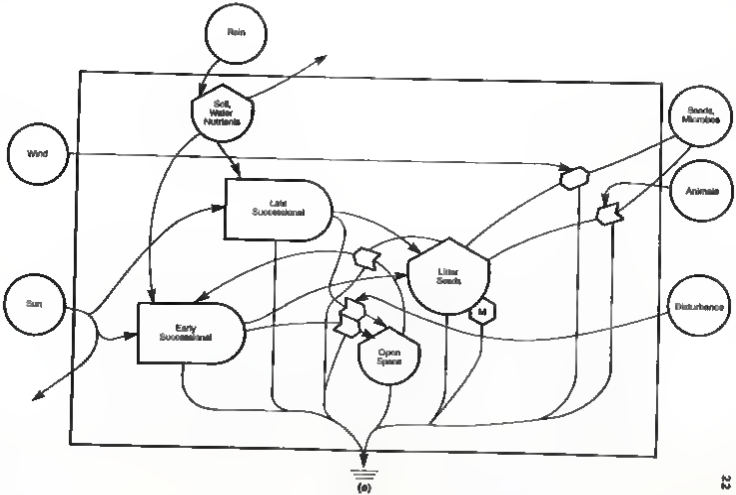
Competing Paradigms of Succession

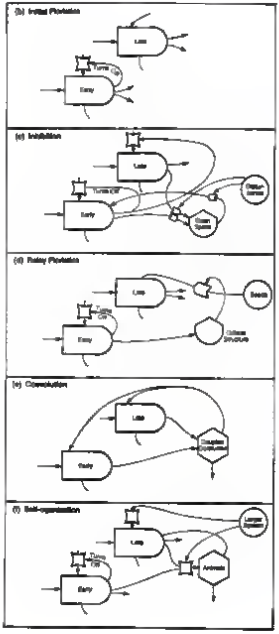
The preceding discussions have revesied five competing paradigms of succession: two individualistic, life history-based models (initial floristics and inhibition) and three holistic ecosystem models (relay floristics, coevolution, and self-organization). An energy circuit language diagram of succession is shown in Figure 3a that includes early and late stage plants, seeding, and nutrient recycle. Additional controls and pathways are added to represent various paradigms for the interactions between early and late successional species (Figures 3b-3f). The concept of each paradigm is briefly summarized below.

Initial floristics. Early and late successional species coexist with the same resources (Figure 3b). The early species modify the site so that it is not suitable for their continued reproduction, but have no effect on the recruitment of late species.

Inhibition. Early and late successional species compete for available space and resources, such as light, nutrients, and moisture (Figure 3c). Rapidly dispersing, fast growing early species colonize available open space and capture available resources, inhibiting the establishment of later

Figure 3. Energy systems diagram of succession: (a) with some of the main pathways of organization, seeding, and nutrient cycle; (b) control in "initial floristics"; (c) control with inhibition; (d) control with "relay floristics"; (e) control with coevolution, pathways permanent; and (f) controls free self-organization and reinforcement from animals and larger surrounding system.


Rain
Soil, Water Nutrients
Wind
Seeds, Microbes
Animals
Late Successional
Litter Seeds
Sun
Early Successional
Disturbance
Open Space
(a)


(b) Initial Protection
Late
Turns Off
Early
(c) Inhibition
Late
Turns Off
Early
Other cells
Host Cells
(d) Relay Protection
Late
Turns Off
Early
Inhibit SHARE
(e) Coordination
Late
Early
(f) Self-organization
Late
Turns Off
Early
Activate

species. Slower growing late successional species can only become established when the early colonizers have been killed or disturbed.

Relay floristics. Late successional species are unable to become established on bare ground; they arrive and become established only after some critical level of development has been reached (Figure 3d). Late successional species gradually displace the early colonizing species. Competition for light results in poor growth and reproduction by early colonizing species, when later successional species are established.

Coevolution An expanded version of the relay floristics model that also recognizes a long-term relationship between species (e.g., feedback relationships between and among trophic levels) (Figure 3e).

Self-organization Producers, consumers, and decomposers are linked in a dynamic feedback network in which each trophic level is composed potentially of many species. Actual species composition of the community is a function of the system's self-organizing choices, which reinforce those combinations that optimize the use of resources and maximize productivity (Figure 3f). Controls and reinforcement are shown from animals and larger scale phenomena of the surrounding system.

Changes in Paradigms

The continuing contradictions about succession after many decades of study suggest that more may be involved than a

straightforward, objective, scientific consideration. Ecology and the succession concept may be in the midst of a revolution (McIntosh, 1983) and specifically a change in paradigms, which Kuhn (1970) has described as the way a scientific discipline progresses.

A common and idealized image of a scientific discipline is that it is universal, objective, and unbiased, with free communication and mutual comprehension among its members. Historians of science show this to be a simplistic and inaccurate view, and discuss the hypothesis of the "invisible college" as the basis of the organizational patterns associated with major advances and changes in paradigms within a scientific discipline (Crane, 1972; Griffin and Mullins, 1972). The invisible college hypothesis argues that any discipline, especially one in a state of change, is subdivided into loose networks of scientists with varying degrees of cohesiveness and continuity. According to Griffin and Mullins (1972) such networks conform to the following criteria:

1. Their members believe they are making major changes in concept or methodology and the word revolution is much in evidence.

2. Members do not consistently observe the attitude of disinterested objectivity typically associated with scientists and may be passionate and one-sided advocates of a "ruling theory."

3. There is commonly a close, even somewhat closed, informal communication network within the network.

4. One or more outgroups are typically recognized and increasingly opposed as the network becomes more tightly organized.

5. A network is commonly identified with a leader who may provide intellectual and/or organizational cohesion. The work that the network associates itself with generally has originated, or is centered on a particular place with a more or less well defined origin and time span.

Some of the confusion and contradictions concerning succession may be attributed to a lack of understanding of the history and sociology of the succession concept and the origins and evolution of the competing paradigms, or conceptual models. Confusion often arises from ignorance, as proponents of a "new" view may be unfamiliar with early work in the field, current thinking within other groups in the field, or their nomenclature and terminology. The invisible college hypothesis may help explain the divergent positions in ecology specifically concerned with succession.

A scientific community upholds an old paradigm in spite of its inadequacies and contradictions until a new and better one emerges and is accepted. The paradigms of succession appear to be flawed and a new paradigm will likely emerge from a more eclectic synthesis. It is clear that an explanation of the cause and mechanism of succession, and development of a reasonable consensus on a paradigm of succession, will require a careful analysis of the historical background, biases and premises, and philosophy of the idea and its practitioners, critics, and proponents.

As a framework for formulating this bridging paradigm, McIntosh (1981) provided a number of questions to be answered:

1. Do the extended observations of succession support a general theory of the successional process that is (a) orderly, directional and predictable; (b) controlled by biotic factors, (ie., autogenic); and (c) leads toward an equilibrium state in either or both its biotic or abiotic attributes?

2. Is the claim of some ecologists that successional phenomena are reducible to theories of natural selection justified? How do population theory and life history strategies explain and predict ecosystem attributes?

3. What are the emergent properties claimed to justify ecosystems theory? If population phenomena are not additive, what is the measure of integration?

4. Does the evolution of ecosystems have any reasonable explanation in evolutionary theory?

5. Is the reduction of ecosystem to trophic numbers, seen by Hutchinson (1942) and Ulanowicz and Kemp (1979) as the essence of the genius of Lindeman, holistic or simply a collective property as stated by Holt (1979)? In what sense is the ecosystem approach to succession holistic?

6. Can reasonably explicit distinctions be made between a small-scale disturbance initiating the traditional serals within the community and a large scale disturbance initiating an earlier stage of a sere? Can autogenic and allogenic disturbances be clearly distinguished or are they interdependent, as suggested by White (1979)?

7. Can a theory of succession be developed to incorporate a sere regularly reaching an equilibrium over an extended area, as argued by Hermann and Likens (1979) and Franklin and Hemstrom (1981), and a sere that is largely interrupted by disturbance as described by Raup (1957) and by Heinselman (1981)? Can the achievement of equilibrium be related to a trajectory toward equilibrium?

Hypotheses and Objectives

Research for this dissertation involved nearly 4 years of field work on mined lands in Polk County, Florida. The main objectives were (1) to evaluate the process of initial

plant community establishment in wetland and terrestrial communities and interpret the results and observations through competing paradigms of succession (initial floristics, inhibition, relay floristics, coevolution, and self-organization), (2) to determine the role played by mound-building ants in the developing community and assess this role with the prevailing paradigms, and (3) identify possible techniques for enhancing succession on strip-mined land. These overall research objectives were addressed in three separate but related field studies.

Marsh Development

Seed bank survey. As an initial step in understanding and enhancing the design of self-maintaining ecosystems, seed bank dynamics were examined. A survey was made (1) to assess the size and species composition of seed banks in selected marsh ecosystems from natural and post-mining landscapes, (2) to identify the ecological role and significance of seed banks in marsh community dynamics, and (3) to evaluate the feasibility of establishing marsh ecosystems by helping form seed banks.

Marsh transect study. Transects were used to compare the herbaceous component of the wetland that developed from natural processes to that created by spreading muck from an onsite donor marsh. Stages of vegetation establishment were

examined to test the hypotheses that (1) differences in the initial floristics in the two treatment areas (mucked versus unmucked) result in communities of very different species composition and (2) differences in the perennial macrophytes of the two different treatment areas would be maintained through time.

Both seedbank and transect studies were used to evaluate the Gleasonian model of wetland succession proposed by van der Valk (1981).

Upland Forest Development

Upland forest studies examined the relationships between early colonizing plants and late successional trees on an unvegetated upland site. The colonizing annuals, biennials, perennials, and low shrubs found on old fields were designated early successional species. The interactions between early and late species were examined to determine which paradigms explained ecosystem development (inhibition, initial floristics, or relay floristics). Field plot experiments using species removal and addition were designed to determine the effect, if any, of colonizing vegetation on establishment, growth, and survival of tree species.

Four treatments were used: (1) natural colonization, (2) enhanced colonization with seeds of several common old-field weeds, (3) addition of legume species, and (4) periodic weeding to keep the plots generally free of any colonizing

vegetation. In both the enhenced colonization end enhenced legume treatments, the natural colonization process was also allowed to occur. Criteria for accepting or rejecting the competing paradigms are given below.

1. If seedlings grew better with either the enhenced colonization, natural colonization or legume treatments, then the initial floristics and inhibition paradigms were rejected in favor of the relay floristics paradigms.

2. If seedlings grew better in weeded plots, then the initial floristics and relay floristics paradigm were rejected in favor of the inhibition model.

3. If seedlings grew about the same in the weeded plot as in other treatment plots, then the relay floristics and inhibition paradigms were rejected in favor of the initial floristics.

Mound-Building Ants and Ecosystem Development

Early successional mined lands provide an opportunity to investigate interactions between species as the community is developing in a simple system with a few producers and a few consumers. Three field observations aroused interest in the role and effects of mound-building ants in such a system.

First, fire ants (Solenopsis invicta) are one of the earliest arriving invertebrate consumers on young strip-mined lands. In central Florida, fire ant populations were usually well established in the first year after mining ceased.

Second, herbaceous plants, especially grasses, growing on ant mounds were typically more robust, with a richer green color than plants found on adjacent non-mound soil. This

observation led to the hypothesis that mound soils were more fertile because of the ants.

Third, it was noted that overburden soils high in clay formed surface crusts that inhibited water infiltration, but mound building and tunneling by ants broke the surface crust and maintained the soil in a more friable condition.

Fire ants are omnivorous scavengers who forage the landscape, gathering food materials and returning with them to the mound. This activity concentrates otherwise dilute nutrient materials, which may be one of the primary functions of ants in the ecosystem. If ant mounds represent a localized concentration of nutrients in the form of insect parts, plant parts, feces, and waste products, then they are also likely to be foci of microbial activity mineralizing organically bound nutrients. The ant colony and mound system may recycle materials that are scarce in the developing ecosystem.

Mound-building ants may alter the soil profile and influence particle size distribution, bulk density, porosity, and infiltration capacity. These soil alterations may affect primary production.

Relationships are shown in diagrammatic form. Arrows on a causal loop diagram of the ant model indicate pathways of influence (Figure 4). A "+" used at an arrowhead indicates an increase in the adjacent item. For example, a larger concentration of food materials in the mound leads to a higher level of microbial decomposers. A "-" indicates a

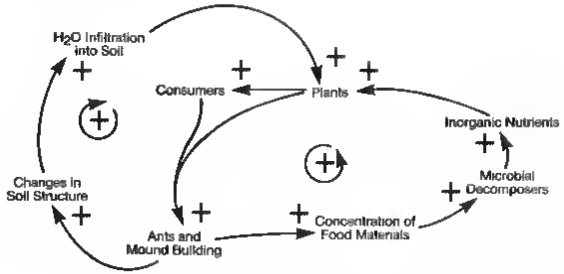


Figure 4. Causal loop diagram showing feedback relationships between mound-building ants, plants, other consumers, water infiltration, soil development and nutrient cycle.

decreases in the item at the arrowhead. The ant model depicts two positive feedback loops, one linking plants-ants-microbes and one linking mounds-soil-water infiltration. The arrows represent causal relationships that can be experimentally evaluated.

An energy circuit language formulation of the ant model (Figure 5) also provided a summary of ecosystem components and energy/material pathways for directing research efforts. Research questions were:

1. Do mound-building ants concentrate nutrients in the landscape?
2. If they do concentrate nutrients, does this provide a feedback to the primary producers (plants), establishing a non-trophic interaction or indirect effect and eventually a feedback to themselves?
3. What function does mound-building work serve for the developing ecosystem?
4. If ants are found to provide positive feedback to the developing ecosystem, are there ways to further stimulate feedbacks and enhance succession?

Description of Study Sites

Eight study sites in central Florida were used in the three phases of the research (see Table 1 and Figure 6). Seven of the sites were within Polk County and one in the northeast Manatee County in the Four Corners area. A brief description of each site is provided below.

Pasture Marsh. This marsh was approximately 1.0 hectare in size and located on the Mobil Chemical Company's

Figure 5. Energy circuit language diagram of ant model.

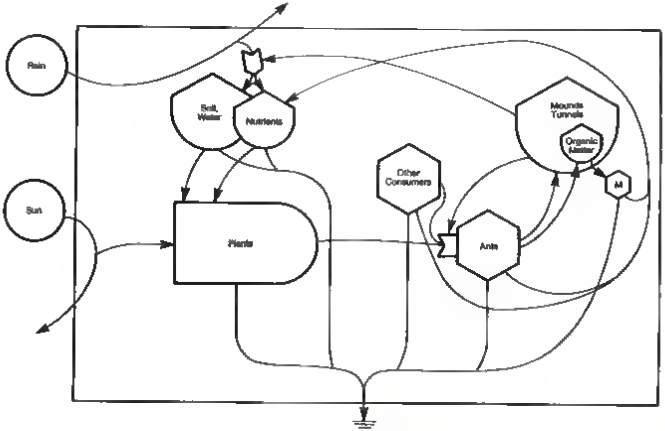

Rain
Sun
Soil, Water
Nutrients
Plants
Other Consumers
Ants
Mounds Tunnels
Organic Matter
All

Table 1. Sites used in marsh study, upland forest study, and ant study.

Sites	Marsh Study	Upland Forest Study	Ant Study
Sanlan Marsh	X		
Tiger Creek Reclamation Area			X
Clearsprings Wetland Demonstration Project	X		X
Whiddon Creek Reclamation Area		X	
Four Corners Wetland Demonstration Project	X		
Fort Green Wetland Demonstration Project	X		X
Natural Marsh	X		
Peace River Bay Swamp	X		

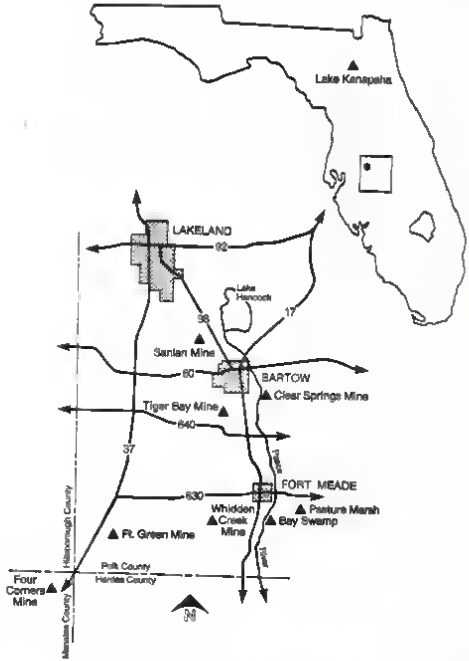


Figure 6. Location of study sites in Polk and Manatee Counties.

South Fort Meade Mine tract. The vegetation within the marsh was dominated by softrush (Juncus effusus), pickerelweed (Pontederia cordata), Sagittaria lancifolia, and smartweed (Polygonum punctatum). The marsh was selected as typical of the freshwater marshes within the study area, most of which are subject to grazing.

Peace River Bayhead. This bay swamp is located on a seepage slope draining to the Peace River on Mobil's South Fort Meade Mine tract. The swamp had an overstory of sweetbay magnolia (Magnolia virginiana), red bay (Persea palustris), and dahoon holly (Ilex cassine). The groundcover consisted primarily of lizard's-tail (Saururus cernuus) The substrate consisted of a layer of finely decomposed muck overlying fibrous peat. The depth of the organic soil averaged approximately 1 m.

Saplan Marsh. This marsh developed on an unreclaimed clay settling area that was mined in the early 1950's. The site was selected because it was one of the few old, unreclaimed clay settling ponds that was not dominated by cattail, primrose-willow, or willow.

Four Corners Demonstration Project. W.R. Grace Company initiated a wetland reclamation demonstration project at its Four Corners Mine site in 1979. Four 0.16-ha depressions were excavated to a maximum depth of 1.2 m in a pine-palmetto flatwoods adjacent to Alderman Creek in 1978. The area was not mined, but overburden was removed to a depth below the

minimum design grade and then backfilled, simulating reclamation. Four test plots were established as follows:

1. Plot 1. Control plot, graded and left for natural revegetation.

2. Plot 2. Hand-planted with plant material taken from nearby natural marsh, including maidencane (Panicum hemitomon), pickerelweed (Pontederia cordata), and Juncus effusus.

3. Plot 3. Mulched 30 cm deep with donor muck from a nearby marsh.

4. Plot 4. Tree plot where 95 trees comprising 16 different species were transplanted from a donor site on Alderman Creek.

Whidden Creek Reclamation Area. The Whidden Creek area was mined by Gardinier Phosphate in 1982 and 1983. The area was reclaimed in 1983 using an integrated landscape approach, that sought to create a small drainage basin discharging to Whidden Creek.

Tiger Bay Reclamation Area. The Tiger Bay area was mined by International Chemicals and Minerals, Inc. (IMC) in 1982 and 1983. The area was reclaimed in 1983 as a sand-and-lakes area typical of the industry's reclamation practice.

Clearsprings Wetland Demonstration Project. Work on this 14-ha wetland demonstration project began in 1978. The project was a joint effort of IMC, the Florida Game and Freshwater Fish Commission, and the U.S. Fish and Wildlife Service. The site adjoins the Peace River and was designed to establish physical site characteristics similar to those that produce and maintain floodplain wetlands. Basins were

created to encourage emergent plants, store water onsite, and create fish and wildlife habitat. Test plantings of 15 different tree species, planted as bare root seedlings were done in 26 plots with 400 trees per plot. Freshwater macrophytes were also planted in the basins.

Fort Green Wetland Demonstration Project. This wetland project is part of a 148-hectare reclamation project carried out by Agrico Mining Company at its Fort Green Mine in southwestern Polk County (Figure 6). The site, which was mined in 1978 and 1979, was recontoured to create 61 ha of wetlands and 87 ha of uplands (Figure 7). The reclamation began in 1981 and was completed by May 1982. The project sought to create open water, freshwater marsh, freshwater swamp, and upland habitat.

The site is gently sloping with a range of 40.23 m down to 35.40 m mean sea level (msl) in the wetland basin. The wetland basin receives runoff and baseflow from the surrounding uplands. The basin has a highwater discharge to the adjacent floodplain of Payne Creek when the surface water elevation reaches approximately 36.58 m msl. Within the wetland basin are several deep holes that serve as deep water habitat and aquatic refuge during times of drought. These deep pools have spot elevations ranging from 31.85 to 35.36 m msl.

The donor muck was transported from a nearby donor marsh and spread in the littoral zone with depth varying from 2.5

to 30 cm. Approximately 15 percent of the litteral zone received the muck treatment.

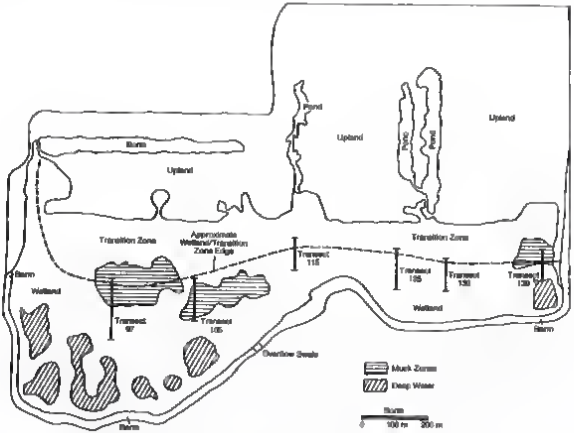


Figure 7. Fort Green wetland reclamation area showing marsh transect locations, approximate vegetation zones, and muck treatment zones.

METHODS

Marsh Development

Seed Bank Survey

The seven wetland sites sampled in the seed bank survey include natural wetlands, and unreclaimed and reclaimed wetlands on mined lands (Table 2 and Figure 6). At each site, one to several major vegetation zones were sampled with a 5-cm diameter, hand core sampler that was pushed into the substrate to the mineral soil layer. The depth of any overlying organic layer was noted, and only the upper 10 cm of the core was retained. Four individual cores were combined to yield a composite sample, with three composite samples taken in each vegetation zone selected. Samples were stored in sealed plastic bags at 4°C until they were processed.

All live plant material was removed from the samples to prevent confusing in seed germination results with any vegetative regeneration. Once the plant material was removed, the samples were placed in wooden flats (25 cm x 25 cm) containing approximately 4 cm of sterilized gravel mixed with tailings sand; the samples were approximately 2 cm deep when spread out evenly in the flats. The flats were then placed

Table 2. Sample locations and site characteristics.

Site	County	Vegetation Zone	Substrate
Unreclaimed Mine Site			
Sanlen marsh (30 yr old)	Polk	*Juncus-Polygonum*	Clay
		Eichhornia	Clay
Reclaimed Mine Sites			
Clearspringe (4 yr old)	Polk	*Polygonum-Ludwigia*	Clay-overburden
Fort Green (2 yr old)	Polk	*Pontederia* (Muck zone)	Muck-overburden
		Open water (Muck zone)	Muck-overburden
		Open water	Overburden
Four Corners Marsh (5 yr old)	Manatee	*Pontederia* (Muck zone)	Muck-sand
		Pontederia (Planted)	Sand
		Eleocharis (Control)	Sand
		Polygonum-Ludwigia	Sand
Natural Wetlands			
Pasture marsh	Polk	*Pontederia-Juncus*	Muck-sand
Peace River bayhead	Polk	*Saururus*	Peat
Lake Kanapaha *	Alachua	*Amaranthus*	Muck-sand
		Echinochloa	Muck-sand
		Open water	Muck-sand
Four Corners marsh	Manatee	*Pontederia-Juncus*	Muck-sand

* Lake Kanapaha not sampled in this study, results from previous study provided by Dr. Ronald Myers

outdoors in large plastic tubs containing sufficient water to maintain a saturated soil condition.

Seedling emergence by species was monitored through time. Unidentified seedlings were counted, transplanted to flower pots, and allowed to mature until they could be identified.

Marsh Transect Study

Six permanently marked transects were established in October 1982. three each randomly located within the muck treatment areas and the unmucked, overburden areas (see Figure 7). All transects began in the shallow littoral zone and extended upslope through the transition zone to the upland edge. The three muck treatment transects totaled 309 m and the three overburden transects totaled 275 m. The difference in total length of the two treatment groups was a result of the slope differences at the random locations.

The plant communities along the transects were monitored using a modification of the standard line-intercept method (Phillips, 1959; Smith, 1980; Canfield, 1941) to record the percent cover by species along each transect. The standard method consists of taking observations along a transect line and noting the identity of any plant touched by an imaginary plane extending vertically above and below the transect line. The distance, or interval, of the plane intercept is also recorded. The individual intervals are totaled for each

species to yield total cover, which can be standardized to percent cover.

The modification of the standard method used in this study consisted of identifying patches or intervals of species occurrence even when the cover by the particular taxa within the patch was less than 100 percent. With this modified line-intercept technique, the interval distance as well as the percent cover by the taxa within the interval was recorded. The modification provided a more rapid method of measurement that was also relatively accurate and well adapted to measuring changes in vegetation across zones and following changes through time.

The transects were sampled over four growing seasons: November 1982; May, July, and November 1983; March, July, and November 1984; and June 1985.

Elevations along each transect were measured on 1.5 m intervals. These elevations were converted to mean sea level (msl) based on a reference to the measured surface water level in the wetland basin that day. A continuous water level record was provided by a surveyed, permanently mounted water level recorder. The daily summary values for the period of study were supplied by Agrico Mining Company.

Upland Forest Studies

An upland area on the west side of Parcel 6 at Gardinier Phosphate Company's Whiddan Creek Mine (Figure 6) was cleared in late October 1983. The cleared area was 63 m by 63 m with a gentle slope from the south to the north. Seedling and direct-seeded plots were located in early December 1983 and two experiments were set up adjacent to each other (Figure 8). The experimental design was a nested analysis of variance with four experimental treatments: colonizing species allowed, colonizers weeded out, colonizers added, and legumes added. Within each of the two experiments were four replicates for each treatment, for a total of 32 plots. All treatments were randomly assigned to plots.

The experimental treatments used in both the seedling and direct-seeded plots were the addition of seed of four colonizing species, the addition of seed of four legume species, the removal of all colonizing species through weeding, and a natural invasion of colonizing species. The first two treatments involved the application of seed, which was completed just prior to planting the tree seeds or seedlings. The initial site clearing in October left all plots free of vegetation at planting time.

The enhanced colonizer treatment included four of the most common species found on old fields and abandoned mine lands in central Florida: natal grass (Rhynchelytrum repens),

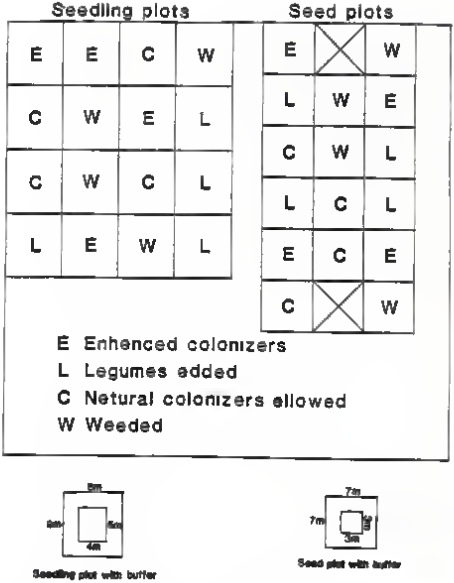


Figure 8. Schematic layout of seed and seedling transplant plots on upland study site at Gardinier's Whidden Creek Mine area.

groundsel (Baccharis halimifolia), dogfennel (Eupatorium capillifolium), and broomsedge (Andropogon virginicus).

Four species were added in the enhanced legume treatment: Cassia obtusifolia , Sesbania macrocarpa, Sesbania punicea, and Sesbania vesicaria. In the direct-seeded plots, 50 seeds of each legume were added for a total of 200 seeds per plot. 110 seeds per legume, totalling 440 seeds per plot, were added to seedling plots receiving this treatment. In both cases, the seeding rate gave a density of 22 legume seeds/m^2.

Seeds for the enhanced colonizer and enhanced legume treatments were applied by mixing the seeds with some overburden soil from the plot and hand broadcasting the mixture onto the plots. The soil was disturbed by hand with rakes and cultivators, to mitigate the effects wind would have on surface spread seeds of these wind-dispersed species. All plots were subsequently disturbed as part of a preplanting treatment. Planting and preplanting treatments were carried out in December 1983.

The weeding treatment was administered quarterly in March, May, June, and September for both the transplanted and direct-seeded plots. All colonizing plants were hand-weeded and removed from the plots.

Heavy rains in the first month after planting created several erosion rills running through the plots. To prevent cross contamination by seeds washing out of one plot and into another, hay was spread on the margins of all plots that had

downslope neighbors. All major erosion rills on the site were mapped as an aid to interpreting results. In addition, several rills that had developed through the seed plots were diverted to interplot areas with a shallow, diversion trench. Once colonizing vegetation began to appear in early spring of 1984, it afforded a modest degree of soil stabilization and the severity of the erosion diminished considerably.

Direct-Seeded Plots

Seeds of seven species were used in the direct-seeded test plots seeds. sweetgum (Liquidambar styraciflua), cabbage palm (Sabal palmetto), live oak (Quercus virginiana), laurel oak (Quercus laurifolia), southern magnolia (Magnolia grandiflora), sugarberry (Celtis laevigata), and pignut hickory (Carya glabra). These seven taxa were considered representative of common mesic hardwood species of central Florida.

The seeding rate per plot was 50 seeds per species, yielding 350 seeds per plot. Each plot planting area was 9 m^2 (3 m by 3 m), resulting in a density of 39 seeds/m^2.

The plots were arranged in a 6 by 3 grid with two of the plots remaining unused (see Figure 8). Treatments were assigned randomly to the plot grid. Each total plot was 7 m by 7 m, which allowed for a 2-m buffer all around the 9m^2 planting area. The seed mix was hand broadcast onto the plots after the soil was disturbed, and the treatment seeds were

added if required were. The plots were then raked lightly to incorporate the seeds into the substrate.

The seed plots were measured in March and October 1984 and the species, height, and growth condition of each seedling in each plot was recorded. The location of each seedling was recorded as well so the fate of individuals could be followed.

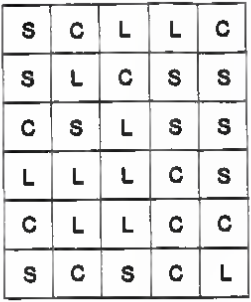
Seedling Transplant Plots

In the seedling test plots, three mesic hardwood species were used: sweetgum, live oak, and cabbage palm. The planting stock for sweetgum and cabbage palm was 8-month-old containerized seedlings grown in overburden soil. The oak seedlings were 1-month-old bare root seedlings.

Ten individuals of each species were used in each of the 16 seedling plots, yielding 30 trees per plot and 480 seedlings total. Tree seedlings were planted after the soil was disturbed and any treatment seeds were added. The 30 trees were randomly assigned to the grid, and the same planting schematic was used in all the plots (see Figure 9).

The total area of each seedling plot was 8 m by 9 m, allowing for a 2-m buffer around an actual planted area of 4 m by 5 m. Seedlings were planted on approximately 1-m centers.

The severe winter freezes of December 1983, and January February 1984 killed many of the planted seedlings. As the



Seedlings planted on 1m centers

C Cabbage Palm
S Sweetgum
L Live Oak

Figure 9. Schematic for planting in Gardinier seedling plots.

freezes occurred before any possible treatment effects could have been exerted, all of the freeze-killed seedlings were replanted on March 27, 1984, which was then used as the starting date for growth measurements on the seedling plots. The plots were measured again in September 1984. At the time of measurement, the height of each seedling and growth condition were recorded

Mound-building Ants and Upland Succession

Survey of Mound Density

Mound densities on the 1-year old IMC Tiger Bay site, the 2-year old Agrico Fort Green site, and the 5-year old IMC Clearsprings site were sampled. Replicate 5 m by 5 m plots were semi-randomly located at each site, and the location, diameter at base, height, general condition, and level of ant activity of each mound within each plot were recorded.

Physical Soil Analyses

Bulk density. Bulk density of mound and non-mound soils at the Fort Green Payne Creek site was sampled with a bulk density core sampler. Seven mound and seven non-mound samples were taken. The samples were oven dried at 103° C until a constant weight was attained, and the density was determined based on the volume of the sampler and its oven-dried weight.

Infiltration tests. Soil water infiltration differences were measured at the Fort Green site using the paired infiltrometer technique (Bertrand, 1965). A metal cylinder, 16.5 cm in diameter and filled with water, was used to measure the rate of water intake of the soil. The metal cylinder was placed on the ground and driven into the soil with a rubber mallet to a depth of approximately 5 cm. A circular berm approximately 10 cm high and 60 cm in diameter was then created around the metal cylinder. The area enclosed by the berm served as the outer cylinder. Both cylinders were maintained at approximately constant head, or depth, by the addition of water. The amount of water lost through the inner cylinder over a measured time interval provided an estimate of the infiltration rate. The infiltrometer test was not designed to measure absolute infiltration rates but rather as a measure of relative infiltration rates in side-by-side comparisons. Three such comparisons were made. The first used three infiltrometers, with one placed over an ant mound, one on an adjacent grassed area typical of the site, and a third on a bluegreen algae flat. This test was run for 120 minutes. The second test, which lasted 60 minutes, compared the rates of another ant mound and another "typical" grassed area. The third test, which lasted 20 minutes, paired another mound and "typical" grassed area.

Chemical Soil Analyses

To test the hypothesis that the activity of the fire ants changes the chemistry of the mound soil relative to the nearby soil, paired soil samples were taken at the Tiger Bay, Fort Green, and Ciearsprings reclamation sites. Each reclamation area consisted of recontoured overburden. Six paired samples were taken, each pair consisting of a mound sample and non-mound sample from 1 m away, were taken at each site. All samples were taken with a bucket auger and stored in plastic bags at 5° C.

Samples were air dried and sifted through a No. 20 mesh sieve to remove ants from the mound soils. A subsample of approximately 100 g was taken from the sieved samples to be used for chemical analysis. The remaining soil was composited to yield single mound and non-mound sample from each of the three sites. The composite samples were used for greenhouse experiments assaying growth differences between the two soils.

Individual soil samples were analyzed for pH, organic matter content, total kjeldahl nitrogen (TKN), and selected cations (calcium, magnesium, potassium, sodium, and manganese).

pH measurements were made with a pH meter with glass electrode in a 2:1 deionized water to soil dilution, using 10 g of air-dried soil mixed with 20 ml of distilled water.

Soil organic matter was determined by the Walkey-Black wet digestion method (Black, 1965).

Nitrogen was measured as TKN by the semi-micro kjeldahl procedure, a 1-g sample of air dried soil 7 ml of sulfuric-salicylic acid was added. After each sample was allowed to set for 30 minutes, 1 g of sodium thiosulfate was added and 2 g of catalyst were added. The samples were then heated in a block digester for 5 hours. After digestion, 20 ml of NaOH, 15 ml of boric acid, and 2 drops of indicator were added to each sample. The samples were then distilled to 60 ml, and titrated with 0.05 normal sulfuric acid.

A dilute double acid solution (0.025 N H_2SO_4 + 0.050 N HCl) was used to determine extractable levels of calcium, magnesium, manganese, potassium, and sodium. Cation levels in the extracts were measured by atomic absorption-emission on a Perkin-Elmer model 500 using standard operating techniques (Perkin Elmer, 1980). One ml of a 10,000 ppm (1%) lanthanum chloride ($LaCl_3$) solution was added to each dilution series of extract, which resulted in a 1000 ppm solution (.1%) in each sample. This procedure was necessary to control for interferences by silicon, aluminum, phosphate, and sulfate, which depress sensitivity in analyses for these cations. Equal amounts of lanthanum chloride were also added to standards and controls before analysis.

Plant Growth Study

Several greenhouse experiments were set up to evaluate a potential growth difference between plants grown on mound and non-mound soils. The tests used a common early colonizing grass, vaseygrass (Paspalum urvillei), and a woody plant, sweetgum (Liquidambar styraciflua), as the assay organisms.

The composite soil samples, as described above, were used in the growth experiments. Ten plastic seedling tubes were filled from each of the six composite samples ten plastic. In each group of ten seedling tubes, five received a seedling of vasey grass and five received sweetgum. The tubes were placed in a greenhouse.

At the end of 60 days, the seedlings were harvested and dried at 103° C to a constant weight. Each vasey grass seedling was subsequently divided into above- and belowground portions that were weighed separately. The sweetgum seedlings were divided into root, stem, and leaf components, each of which was weighed separately. Leaf area of each sweetgum seedling was determined by making a xerographic image of the leaves, cutting out the individual images, and measuring leaf area with an automatic area meter.

Statistical Analyses

All statistical analyses were run with the Statistical Analysis System (SAS). Data expressed as percent were transformed by the arcsine function.

RESULTS

Marsh Development

Seed Bank Survey

Results are presented in four general areas: seed bank density, species importance values, floristic similarity between samples, and species diversity of samples.

Seed bank densities. The mean number of seeds germinating in samples from natural, reclaimed, and unreclaimed marshes in central Florida ranged from 1877 to 72,500/m^2 (Table 3). For comparison, seed bank studies of natural wetlands from Florida, Iowa, New Jersey, and Ontario have shown a range of density from 6,000 to 156,000 seeds/m^2 (Table 4). The overall range of seed bank size (density) covers three orders of magnitude; the lowest density is 1877/m^2 in the sample mucked-unvegetated zone at Fort Green and the high value is 156,000/m^2 from the Sacciolepis striata zone at Lake Kanapaha, Florida.

The range for natural wetlands samples is 4,000 to 156,000 seeds/m^2, with the lowest value from the Peace River bay swamp (the only forested wetland sample) and the high value again for the Sacciolepis zone at Lake Kanapaha. A trend evident in the results from studies at Lake Kanapaha is

Table 3. Mean number of germinating seeds per m²* by species for natural wetlands and reclaimed and unreclaimed marshes in central Florida phosphate district.

	[illegible] Swamp	Four Corners Natural Marsh	Pasture Marsh	[illegible] Juncus [illegible]	 [illegible]	Four Corners Topsoiled Marsh	 Flooded Marsh	 Control Marsh	 Flooded Swamp	Clear Springs South Basin [illegible]	 South Basin [illegible]	 North Basin	[illegible] Topsoiled Vegetated	 Topsoiled Unvegetated	 [illegible]
Aster subulata										15	400	310			
Baccharis halimifolia										125	[illegible]	300			
Carex sp					125										
Cyperus [illegible]					[illegible]					51					
Cyperus sp.													[illegible]	[illegible]	[illegible]
Cyperus [illegible]	54			[illegible]	[illegible]	[illegible]			300	1 455	4,135	1,200			
Cyperaceae I												[illegible]			
Echinochloa walteri															115
Eclipta alba				[illegible]						[illegible]	[illegible]	[illegible]			
Eupatorium [illegible]	84			341				136	[illegible]	[illegible]	200	375		43	[illegible]
Gnaphalium [illegible]										[illegible]					
Grasses unknown [illegible]			43						125						
[illegible]									43						
[illegible]							[illegible]								
[illegible]	[illegible]										250	100			
[illegible]										1 430					
[illegible]		43	[illegible]												
Hydrocotyle verticillata	43														
Hypericum [illegible]	43											140			
Juncus effusus	202	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Juncus [illegible]	[illegible]			35		42									
Ludwigia [illegible]	[illegible]									300	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Ludwigia [illegible]	[illegible]									42					
Ludwigia leptocarpa										[illegible]	[illegible]				
[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		43	[illegible]	[illegible]	[illegible]			
[illegible]										25	[illegible]	[illegible]			
[illegible]											[illegible]				
[illegible]	[illegible]											43			
Scrophulariaceae I										[illegible]					
[illegible]								[illegible]							
Unknown species [illegible]										[illegible]	[illegible]	2,300	275		
[illegible]							[illegible]	[illegible]	[illegible]						
[illegible]	[illegible]													[illegible]	[illegible]
Mean # seeds/m2	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
# species	11	[illegible]	1	3	3	1	4	4	1	15	11	11	4	1	1

*Results from core samples [illegible] cm [illegible] with actual area sampled corrected to standard reference area of 1 m²

Table 4. Seed bank densities, species richness, and Shannon-Weaver diversity index from Florida wetlands and selected marsh studies from temperate North America.

	Mean # seeds/m²	Number of Species	Shannon-Weaver Diversity H'	Source
Natural Systems, Florida				
Bay Swamp	4,325	32	1.48	This study
Lake Kanapaha				
Sacciolepis zone	150,000	36	2.84	Myers 1983
Amaranthus zone	20,000	17	1.72	Myers 1983
Echinochloa zone	30,000	11	0.98	Myers 1983
Pond zone	5,000	0	3.17	Myers 1983
Four Corners Marsh				
Juncus-Pontederia zone	72,502	3	0.00	This study
Pasture Marsh				
Juncus-Pontederia zone	41,250	4	0.28	This study
Reclaimed Systems				
Sanlan				
Juncus-Polygonum Marsh	62,250	8	0.30	This study
Eichhornia Marsh	12,040	5	0.00	This study
Reclaimed Systems				
Four Corners Reclamation Project				
Mulched plot	33,000	4	0.05	This study
Slanted plot	33,710	4	0.05	This study
Control plot	2,210	4	0.55	This study
Slanted swamp plot	11,460	4	0.30	This study
Clearsprings Reclamation Project				
South Basin #1	7,375	10	2.03	This study
South Basin #2	11,300	13	1.92	This study
North Basin	9,880	14	1.88	This study
Fort Green Reclamation Project				
Mulched vegetated	3,334	4	1.13	This study
Mulched unvegetated	1,877	5	0.24	This study
Unmulched	3,520	0	1.30	Thisstudy
Other Natural Systems				
Iowa, Prairie glacial marsh	20-40,000	7-10	Not calculated	van der Valk and Davis (1978, 1979)
Ontario, Lakeshore marsh	0-20,000	31	Not calculated	Keddy and Reznicek (1982)
New Jersey, Freshwater tidal marsh	0-32,000	12-20	Not calculated	Leck and Graveline (1979)

that the species richness and size of the seed bank appear to decreases as the water depth increases in the Sacciolepis zone-Amaranthus zone-Echinochloa zone-Pond zone (Table 4). For the wetland samples cited from outside Florida, the densities range from 6,000 to 40,000/m^2, and for the three natural systems sampled in this study, the range of densities is 2,000 to 72,000/m^2. The two marsh samples (Four Corners natural marsh and pasture marsh) had densities of 41,000/m^2 and 72,500/m^2, respectively.

The unreclaimed wetland sampled, the Sanlan marsh, had densities of 12,000/m^2 and 62,000/m^2 from the Eichhornia and Juncus marshes, respectively. As with the Kanapaha samples, seed bank size apparently decreases with depth (water depth is more than a meter in the Eichhornia marsh). The Sanlan samples, especially the Juncus-Polygonum zone with 62,000/m^2, fall in the range of the natural wetlands already discussed, thus representing some of the higher densities encountered. This indicates that sizeable seed banks can develop in the absence of any reclamation efforts in post-mining wetlands.

Wetland samples from reclaimed mine lands had a range of 1,800 to 33,000/m^2, which is low to moderate by comparison to natural wetland systems. Samples from the three basins at Clearsprings ranged from 7,000 to 11,000/m^2; at the Four Corners project, the range was 2,200 to 33,000/m^2. More specifically, the treated plots had densities well within the range of the natural systems: topsoiled (peat) marsh plot

(33,000/m^2), planted marsh plot (31,000/m^2), and swamp planted plot (11,300/m^2). The lowest density found at the Four Corners project came from the control plot (2,200/m^2), indicating that seed bank establishment is facilitated by reclamation efforts.

Samples from the Fort Green project had the lowest and narrowest range of densities (1,800 to 3,900/m^2), but it should be remembered that this project is only in its second growing season. Surprisingly, the lowest density value from Fort Green, and for all samples, came from an unvegetated topsoiled (peat) area with open water. This may be a result of the vagaries of sampling; alternatively, the seed bank in the peat at this spot may be dominated by short-lived seeds or species that only germinate under flooded conditions (which were not duplicated in this study) or the topsoil material (peat) may have been stockpiled (as is known to have occurred with some peat material at this site).

Species importance values. As an estimate of the overall influence or importance of each species in the seed bank survey, modified importance value were calculated from the density and frequency totals (Table 5). The importance value is calculated by adding relative density and relative frequency for each species, where relative density is the density of the species divided by the sum of all densities, and where relative frequency is defined as the frequency of

Table 5. Seed bank density data from Table 3 summarized across sites for species totals of density, relative density, frequency, relative frequency, and importance value.

	Density Total (mean #/m²)	% Relative Density	Sampling Site Frequency	% Relative Frequency	Importance Value
Aster subulata	1,128	0.36	0.20	2.80	3.16
Baccharis halimifolia	488	0.15	0.20	2.80	2.95
Carex sp	128	0.04	0.07	0.93	0.99
Cyperus brevifolius	900	0.16	0.13	1.90	2.05
Cyperus sp	2,109	0.70	0.20	2.80	3.50
Cyperus rotundus	13,207	4.00	0.53	7.50	11.50
Cyperaceae ?	84	0.03	0.07	0.93	0.95
Echinochloa walteri	125	0.04	0.07	0.93	0.58
Eclipta alba	930	0.30	0.27	1.80	4.10
Eupatorium coronopifolium	1,672	0.80	0.60	8.90	9.00
Gratiolum obtusifolium	84	0.03	0.07	0.95	0.98
Grasses, unknown #1	197	0.05	0.13	1.90	1.95
Grasses, unknown #2	42	0.01	0.07	0.93	0.97
Grasses, unknown #3	84	0.03	0.07	0.95	0.98
Grasses, unknown #4	417	0.13	0.20	2.90	2.03
Grasses, unknown #5	1,625	0.50	0.07	0.93	1.45
Grasses, unknown #6	128	0.04	0.13	1.90	1.94
Hydrocotyle verticillata	42	0.02	0.07	0.93	0.90
Hyssopus mutilum	200	0.07	0.13	1.90	1.97
Juncus effusus	257,367	84.00	1.00	14.00	98.00
Juncus bufonius	205	0.07	0.20	2.90	2.97
Ludwigia virgata	9,465	3.00	0.47	6.60	9.60
Ludwigia palustris	376	0.12	0.13	1.90	2.00
Ludwigia leptocarpa	294	0.09	0.13	1.90	2.00
Polygonum punctatum	8,386	2.90	0.67	9.50	12.50
Pilularia capillacea	1,168	0.40	0.20	2.80	3.20
Rumex verticillatus	42	0.02	0.07	0.93	0.97
Samolus parviflorus	292	0.09	0.12	1.50	2.00
Scrophulariaceae ?	42	0.02	0.07	0.93	0.95
Stellaria media	324	0.10	0.07	0.95	1.00
Unknown species #1	5,334	1.70	0.27	4.00	5.50
#2	376	0.10	0.20	2.90	2.90
#3	2,790	0.90	0.20	2.90	3.76
Column total	308,803	100.00	7.07	100.00	200.00

occurrence of the species divided by the sum of all species frequencies. Both relative density and frequency were connected. With this type of calculation, both relative frequency and relative density are constrained to values between 0 and 100 percent, which produces an importance value for each species in the range 0 to 200.

The most striking aspect of the calculations was the numerical dominance of soft rush (Juncus effusus), which accounted for 84 percent of the germinating seeds in the study. It was also the only species found in all samples, yielding an absolute frequency of 1.0.

The 20 species of highest importance value account for 92.5 percent of the total importance value (see Table 6). In fact, the four species of highest importance value soft rush, smartweed (Polygonum punctatum), Cyperus rotundus, and Ludwigia virgata account for 94 percent of the relative density and 66 percent of the total importance value. These four species can be considered the dominant species in this study and serve in general to characterize the seed banks sampled from central Florida.

Floristic similarity. Floristic similarity of seed bank samples was measured using the similarity index of Czekanowski for binary data. The index is defined as follows:

$$\text{Czekanowski's index} = 2a/(2a + b + c)$$

where a = species common to sites 1 and 2, b = species found at site 1 but absent at site 2, and c = species found at site

Table 6. Twenty species with highest importance values (IV) along with the relative density and relative frequency values used to calculate the IV. All data taken from Tables 3 and 4.

Species	% Relative Density	% Relative Frequency	Importance Value
Juncus effusus	84.00	14.00	98.00
Polygonum punctatum	3.00	9.50	12.50
Cyperus rotundus	4.00	7.50	11.50
Ludwigia virgata	1.00	8.60	9.60
Eupatorium compositifolium	0.50	8.50	9.00
Unknown 1	1.70	3.80	5.50
Eclipta alba	0.30	3.80	4.10
Unknown 3	0.90	2.80	3.70
Cyperus sp.	0.70	2.80	3.50
Ptilimnium capillaceum	0.40	2.80	3.20
Aster subulata	0.36	2.80	3.16
Baccharis halimifolia	0.15	2.80	2.95
Grass 4	0.13	2.80	2.93
Unknown 2	0.10	2.80	2.90
Juncus bufonius	0.07	2.80	2.87
Cyperus brevifolius	0.16	1.90	2.06
Ludwigia palustris	0.12	1.90	2.02
Ludwigia leptocarpa	0.09	1.90	1.99
Samolus parviflorus	0.09	1.90	1.99
Hypericum mutilum	0.07	1.90	1.97
			185.00

but absent at site 1. The index has a range of 0 to 1.0, where 0 represents complete dissimilarity and 1.0 represents complete similarity.

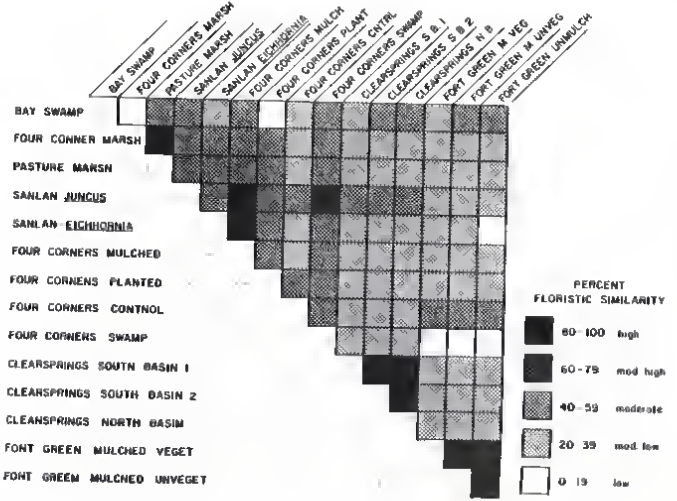
There were few cases of high floristic similarity (Figure 10). One was a comparison between the two natural marshes sampled and another between the Sanlan Juncus marsh and the Four Corners mulched plot, both of which compare samples of with low species richness. The other cases of high floristic similarity are within-site sample comparisons, one from Clearsprings and one from Fort Green.

The Clearsprings samples had the largest number of species and had moderately high to high within-site floristic similarity. The species assemblage at Clearsprings had several unique or less frequently encountered species, including Aster subulata, Baccharis halimifolia, Eclipta alba, and Ptilimnium capillaceum. The samples from Fort Green also exhibited moderately high to high within-site floristic similarity, largely due to three species (soft rush, Ludwigia virgata, and a species of Cyperus).

Many comparisons of low to moderate similarity are noted, primarily because of the near ubiquity of soft rush and smartweed in all samples (Figure 10).

Species diversity. Species richness and species diversity were compiled from data from this study and from Lake Kanapaha (Myers, 1983) (Table 4). Diversity was

Figure 10. Summary matrix of floristic similarity between seed bank samples.


BAY SWAMP
FOUR CORNERS MARSH
PASTURE MARSH
SANLAN JUNCUS
SANLAN EICHHORNIA
FOUR CORNERS MULCH
FOUR CORNERS PLANT
FOUR CORNERS CNTRL
FOUR CORNERS SWAMP
CLEARSPRINGS S B 1
CLEARSPRINGS S B 2
CLEARSPRINGS N B
FORT GREEN M VEG
FORT GREEN M UNVEG
FORT GREEN UNMULCH
BAY SWAMP
FOUR CONNER MARSH
PASTURE MARSH
SANLAN JUNCUS
SANLAN EICHHORNIA
FOUR CORNERS MULCHED
FOUR CORNENS PLANTED
FOUR CORNERS CONTNOL
FOUR CORNERS SWAMP
CLEARSPRINGS SOUTN BASIN 1
CLEARSPRINGS SOUTH BASIN 2
CLEANSPRINGS NORTH BASIM
FONT GREEN MULCHED VEGET
FONT GREEM MULCNED UNVEGET
PERCENT
FLORISTIC SIMILARITY
80-100 high
60-79 mod high
40-59 moderate
20 39 mod low
0 19 low

calculated using the Shannon-Weaver diversity index, given as H' and defined as

$$H' = - (P_i \ln P_i)$$

where P_i is the ratio of the number of individuals of the ith species divided by the total number of individuals in the sample. The value of H' is influenced by two factors: the number of species, known as species richness, and the equitability with which the individuals of the population are apportioned among the species. The greater the species richness or the equitability the greater the value of H'.

The overall range of H' values was 0.05 to 2.64; the lower value was from the mulched, vegetated plot at Fort Green and the highest from the Sacciolepis-zone at Lake Kanapaha. The latter sample also had the highest seed density (156,000/m^2) and the highest species richness (38).

The samples with the greater number of species typically had H' values in the upper range (see Table 4). The most diverse natural wetland samples came from Lake Kanapaha and the bay swamp, while the highest diversity in the mined wetlands group was in the Clearepringe samples. In several cases (Four Corners natural marsh, pasture marsh, Four Corners mulched plot, Four Corners planted plot, and Sanlan Juncus-zone, the seed bank had relatively few species and was dominated numerically by soft rush. This situation more or less defined the low end of the H' range.

Seed bank samples from all but the youngest sites in the post-mining landscape fell within or just below the range of densities and species diversity found in natural wetlands of Florida, Iowa, New Jersey, and Ontario. The indications from the results in this study are that it is possible for nature to reestablish a seed bank of approximately the same size and diversity as that occurring in some natural marshes, such as with the Juncus-Polygonum marsh at Senlen (30 years old). The time required for the seed bank to become a "reasonable facsimile" of a natural marsh as yet may be undefined. The results at Clearsprings indicate that modest sized seed banks with higher diversity can develop in 4 years with little actual marsh reclamation. With some reclamation efforts, seed banks that compare very favorably in size with natural marshes can develop in 5 years, as demonstrated at Four Corners.

The seed banks in some of the post-mining wetlands do not appear to be different in size and species composition from the natural marshes sampled in this study. However, the actual vegetation present is not always as diverse, dense, or well developed, except in cases where muck (topsoil) from a donor wetland was applied. As an example, the results of line-intercept transects in mucked and unmucked areas of the marsh at Fort Green showed that the mucked areas to have 100 percent cover, while the unmucked areas had less than 30 percent cover.

Marsh Transect Study

Water levels and hydroperiod. Daily water levels in the Fort Green wetland were summarized as mean monthly values for the period of the study, August 1982 to December 1985 (Figure 11). Evident trends include the typical annual hydroperiod cycle and the drought that began in late 1984 and continued through late summer of 1985.

The typical annual hydroperiod cycle began with low water in early winter followed by a rise in late winter or early spring and a spring peak. The cycle continued with a summer decline, a late summer peak, and a fall decline. With the exception of the 1985 drought cycle, the annual hydroperiod in the basin has typically varied about 0.3 m between lows of approximately 38.42 m msl to peaks of about 38.67 m msl.

From the fall of 1984 through the spring 1985 a drought occurred that was unrelieved by spring rains. Water levels in the basin declined steadily from August 1984 to June 1985, when they reached a monthly low of 35.37 m msl. The late summer rains of 1985 brought the water level up to the typical late summer peak by August.

The transect elevation data were used to generate individual transect profiles (see Figures 12 and 13). Four of the transects (97, 115, 125, and 130) began at elevations between 38.08 and 38.27 m, while transect 105 started at a lower elevation (35.60 m msl) and transect 139 started at a

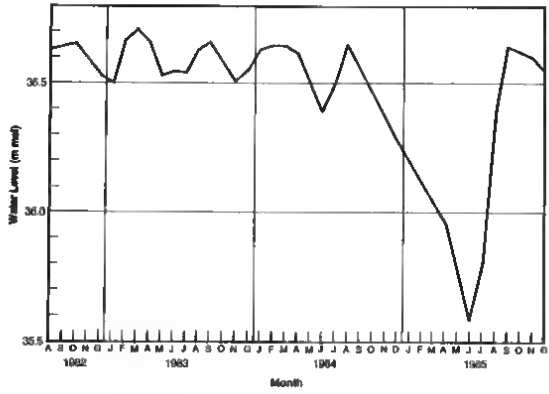


Figure 11. Hydrograph of surface water elevation in Fort Green wetland based on average monthly values for the period August 1982 through December 1985.

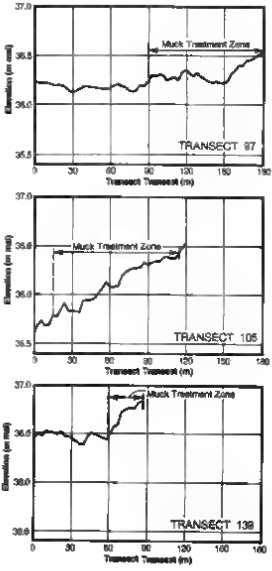


Figure 12. Elevation profiles of marsh transects 97, 105 and 139 with muck treatment zones indicated.

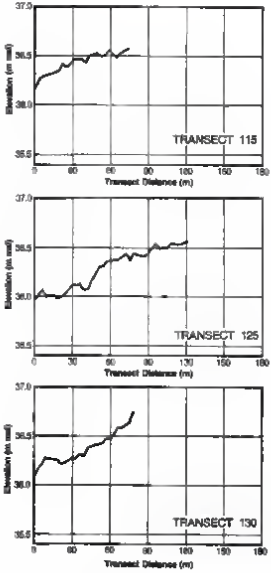


Figure 13. Elevation profiles of marsh transects 115, 125, and 130.

higher elevation (36.45 m msl). Four of the transects ended at approximately the same elevation of 36.60 m msl. The remaining two transects (130 and 139) ended at approximately 36.80 m msl.

The daily basin water levels for the period August 1982 to December 1985 were used to generate a depth exceedence relationship (Figure 14) showing percent of the time a given elevation was inundated. The graph shows a 1.2 m variation in water level during the study period. Elevations below 35.51 m msl were inundated 100 percent of the time and areas above 36.73 m msl were never inundated. The curve slopes gently in the 80 to 100 percent inundation, range which covers a relatively broad range of elevations from 35.51 to 36.33 m msl. The 70 to 80 percent inundation zone covers a relatively narrower elevation range (36.33 to 36.45 m msl). The slope of the depth exceedence curve is fairly steep in the 0 to 70 percent inundation range (elevation 36.33 to 36.73 m msl) then flattens at the maximum inundation of 36.73 m msl.

Emergent Macrophytes. The changes in cover of pickerelweed (Pontederia cordata) and cattail (Typha latifolia and T. domingensis) on each of the six transects through each of the eight sampling periods were summarized from the line-intercept data. Pickerelweed and cattail were used because each was initially the dominant perennial emergent macrophyte in the mucked and unmucked zones, respectively. This

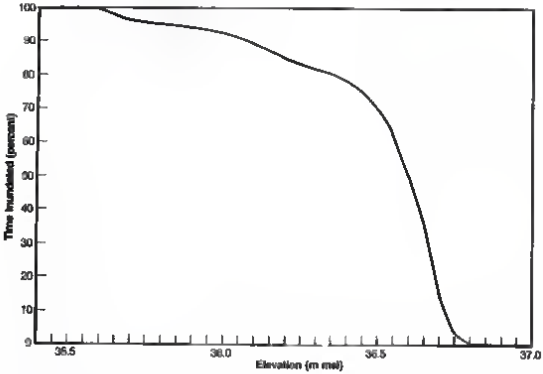


Figure 14. Depth exceedence curve for Fort Green wetland indicating the percent inundation for each elevation over the time period August 1992 through December 1995.

dominance was consistent throughout the study (see detailed vegetation data in Appendix 8).

The time series of cover changes for the two taxa (Figures 15a through 15f) illustrate several aspects of the biology of the two species and differences in the marsh community development in mucked and unmucked areas. Pickerelweed became well established in the mucked zones of transects 97 and 105, but failed to reach the same level of development on any of the other four transects, including mucked transect 139. Conversely, cattail became well established on the overburden transects but lagged in colonizing those areas with well established stands of pickerelweed (transects 97 and 105).

Also, through the first few sampling periods, the sequence of stand establishment is evident for both taxa: (1) initial establishment of individual plants or clumps, (2) expansion of initial clumps, and (3) consolidation of clumps into larger patches or stands. Following the consolidation phase, most of the large clumps remained stable up to the drought of 1985. After the establishment phase, some movement and adjustment to other areas of the transect took place, especially in the case of cattail. This sequence of establishment is well demonstrated on transects 97 and 105 for pickerelweed (Figures 15a and 15b) and transects 115, 125, 130, and 139 for cattail (Figures 15c, 15d, 15e, and 15f). One particular difference between the two taxa is the vagility

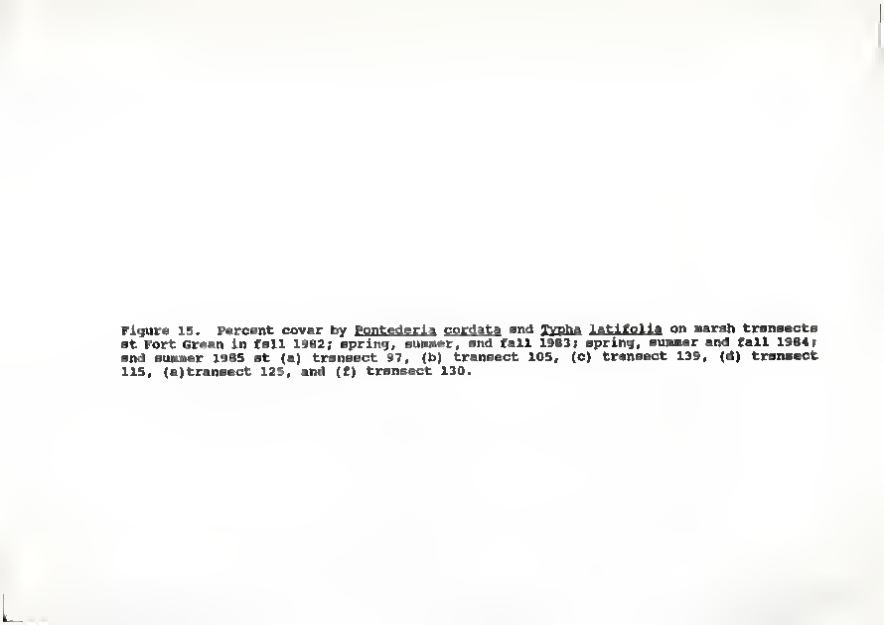
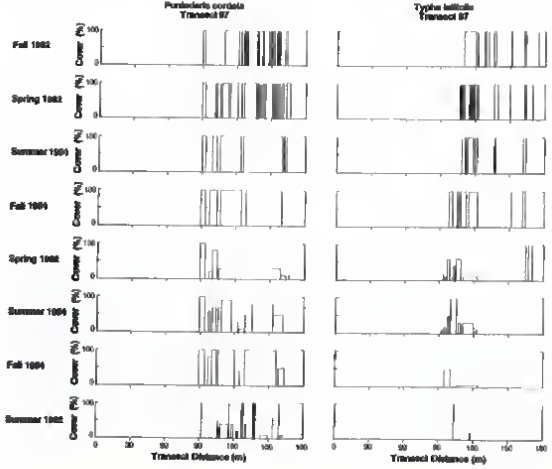


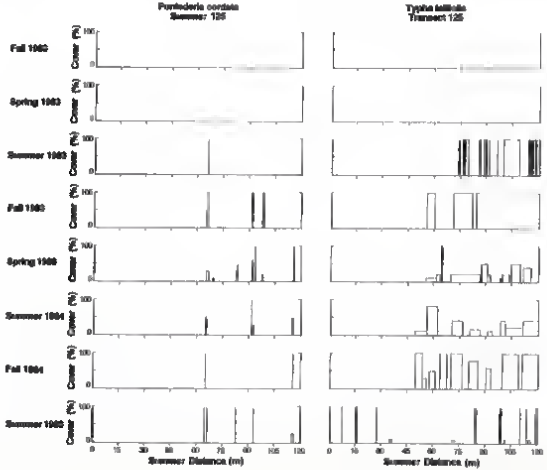
Figure 15. Percent cover by Pontederia cordata and Typha latifolia on marsh transects at Fort Green in fall 1982; spring, summer, and fall 1983; spring, summer and fall 1984; and summer 1985 at (a) transect 97, (b) transect 105, (c) transect 139, (d) transect 115, (e)transect 125, and (f) transect 130.

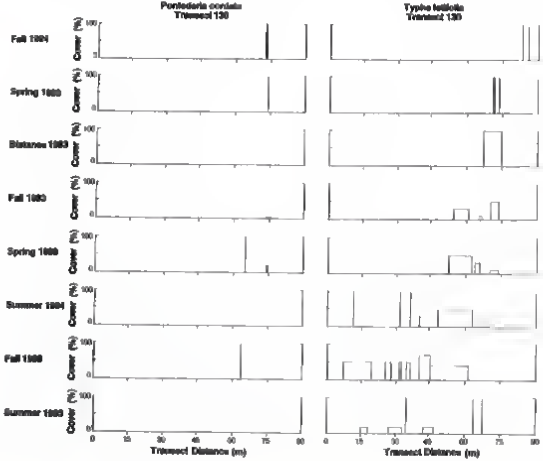

Fall 1982
Spring 1983
Summer 1984
Fall 1984
Spring 1985
Summer 1985
Fall 1985
Summer 1986
Cover (%)
100
0
Panicularis cordata
Transect 97
Typha latifolia
Transect 97
0
30
60
90
120
150
180
Transect Distance (m)

Fall 1992
Spring 1993
Summer 1993
Fall 1993
Spring 1994
Summer 1994
Fall 1994
Summer 1995
Cover (%)
Transect Distance (m)
Phragmites australis
Transect 800
Typha latifolia
Transect 800

Fall 1984
Spring 1985
Summer 1985
Fall 1985
Spring 1986
Summer 1986
Fall 1986
Summer 1986
Count (#)
Trimount Distance (m)
Peridotia cocktail
Trimount 120
Tyche telinda
Trimount 120

Pectoralis cordata
Trimmed 115
Tyrphis latitudo
Trimmed 118
Fall 1988
Spring 1989
Summer 1989
Fall 1989
Spring 1990
Summer 1990
Fall 1990
Summer 1991
Trimmed Eldoracia (m)
Trimmed Eldoracia (m)


Pontederia cordata
Typha latifolia
Transect 125
Fall 1993
Spring 1993
Summer 1993
Fall 1993
Spring 1994
Summer 1994
Fall 1994
Summer 1995
Cover (%)
Summer Distance (m)


Pontederia cordata
Transect 130
Typha latifolia
Transect 130
Fall 1994
Spring 1995
Distance 1995
Fall 1995
Spring 1996
Summer 1996
Fall 1996
Summer 1997
Cover (%)
100
0
0
15
30
45
60
75
90
Transect Distance (m)

of the propagules. Cattail has a very small, wind-dispersed seed; pickerelweed has a heavier, water/animal-dispersed fruit. On several of the transects, cattail was able to colonize new areas as they became available with the falling water levels of the drought of 1985. Cattail appeared more successful at expanding into open habitat than pickeralweed, but other taxa were equally opportunistic, especially bulrush (Scirpus californicus) and dogfennel (Eupatorium capillifolium).

Major changes in the littoral zone vegetation resulted from the drought. The overall species richness and total cover values within the wetland were within the range found in previous periods, but the manner in which the cover was apportioned over the various taxa was significantly different. For both the topsoiled and overburden areas, the cover of many common species declined and dramatic increases in cover were shown by other taxa, especially dogfennel and bulrush.

Dogfennel increased profoundly in cover percentages (25 percent and 18 percent for muck treatment and overburden areas respectively) (Table 7), especially in the deeper areas of the wetland as the water levels receded. At the peak of the drought, most of the area that typically had standing water was vegetated with a well established, monospecific stand of dogfennel by April of 1985. The timing of the dogfennel germination means that the seeds would have had to have been lying dormant in the substrate; as the water level receded,

Table 7. Percent cover of Eupatorium capillifolium and Scirpus californicus on muck treatment and overburden transects, Fort Green marsh, eight sampling periods between fall 1982 and summer 1985.

Sampling Period	Eupatorium capillifolium		Scirpus californicus	
	Muck Transects	Overburden	Muck Transects	Overburden
Fall 1982	0	--	--	--
Spring 1983	0.3	--	--	--
Summer 1983	0.4	0.1	--	--
Fall 1983	0.1	<0.1	--	--
Spring 1984	0.1	0.2	--	0.2
Summer 1984	0.3	0.2	0.2	0.3
Fall 1984	1	0.3	0.8	0.3
Summer 1985	25	10	9	8

the dogfennel seedbank responded and a complete cover developed.

Bulrush also increased in cover at the north end of the basin, as seen in 1985 results from transects 125, 130, and 135. As with dogfennel, the increase occurred in normally flooded areas lacking established emergent vegetation. The area of bulrush invasion was also a site of noticeable invasion by Sagittaria lancifolia and dogfennel. These areas showed little to no invasion by cattail, which was well established in the vicinity and had been spreading vegetatively for the previous two seasons. Bulrush was able to colonize and establish in an area that appeared to be ideal for cattail invasion.

The transect specific elevation profiles and inundation frequencies were used to compare the zones of establishment of cattail and pickerelweed (Table 8). The two taxa do occupy roughly the same zone within the wetland based on the patch establishment (Figures 15a through 15f), from approximately elevation 36.33 to 36.58 m msl and with an inundation range of 40 to 80 percent. The results from transect 105 are particularly interesting because the mulch was spread in deeper areas, down to elevation 35.51 m msl, that were permanently flooded. These deepwater stands were neither invaded nor encroached upon by cattail during the study period. They were also not ephemeral in nature, remaining constant throughout the study although they showing similar

Table 8. Summary of transect distance, elevation range, and inundation frequency of establishment zones for Pontederia cordata and Typha sp. on marsh transects at Port Green wetland reclamation demonstration project, and summary of transect distance, elevation range, and inundation frequency of muck treatment zones on transects 97, 105, and 139.

	Muck Treatment Transects			Overburden Soil Transects		
	97	105	139	105	125	139
Pontederia cordata						
Initial Appearance (distance m)	46 to 135	0 to 134	87 to 87	52 & 82	105	72
Establishment Zone (distance m)	46 to 310	0 to 161	87 to 87	81 to 84	225 & 300	72
Elevation Range (m msl)	36 11 to 36 33	35 36 to 36 00	36 36 to 00 00	36 36 to 36 45	36 0 & 36 51	36 36
Inundation Frequency	36 to 853	79 to 1006	0 to 333	79 to 758	48 to 853	836
Typha sp.						
Initial Appearance (distance m)	815 to 135	79 to 000	00 & 36	00 to 36	84 to 165	22 to 48
Establishment Zone (distance m)	85 to 100	65 to 814	0 to 81	22 to 46	36 to 175	0 to 65
Elevation Range (m msl)	36 22 to 36 36	00 36 to 36 42	36 00 to 36 36	36 00 to 36 36	36 36 to 00 36	36 00 to 36 36
Inundation Frequency	000	00 to 000	45 to 836	00 to 836	00 to 000	00 to 000
Zone Treatment Area						
Treatment Zone (distance m)	36 to 136	0 to 1[3	36 to 36			
Elevation Range (m msl)	36 00 to 36 45	00 36 to 36 36	36 00 to 36 45			
Inundation Frequency	70 to 853	79 to 000	0 to 765			

drought responses. This indicates that macrophytes like pickerelweed can become established in deep water areas and muck application should be extended down to elevations with an average depth of flooding of up to 1 m or more.

Large stands of pickerelweed developed only in the muck treatment areas. Though it produced large numbers of seeds, pickerelweed did not spread far from the areas of initial establishment during the first four growing seasons.

Upland Succession Plots

Seed Germination and Survival

The experiment was originally designed as a nested analysis of variance with a balanced design (i.e., equal replications for each treatment). A sampling mistake during the second weeding event (May) changed this plan, when plot 15 was weeded instead of plot 18. The error was not discovered until the third weeding (June), at which time it was decided to continue weeding plot 18. This change created some difficulties as to the treatment status of plots 15 and 18. To incorporate plots 15 and 18 into the analysis, the analysis of variance (ANOVA) for each species was carried out using two different assignments for the plots: one analysis with plot 15 assigned to weeded treatment and plot 18 dropped and a second analysis with both plots dropped. Analyzing the data following the original plot assignments (15 to enhanced

colonizer and 16 to weeded) was clearly inappropriate, as plot 15 could be no longer be considered as part of the enhanced colonizer treatment after it was weeded, but a simpler solution seemed to be to drop plots 15 and 18 from the statistical analysis altogether. Although an unbalanced design may result, any problems of equivocation over the treatment status of plots 15 and 18 are eliminated. An ANOVA configuration in which plot 15 is assigned to the weeded treatment and plot 18 is dropped is also a fairly clearcut case. As plot 15 was weeded during the later part of the growing season, the seedlings were growing under weeded conditions beyond the germination stage.

The seed plots yielded information on germination, the survival of the germinating seeds, and the growth of the surviving seedlings. Total germination was estimated with data from the two sampling periods in March and October 1984 (Table 9). Because the location of each seedling in the plot was recorded at the time of sampling, the fate of any given seedling could be followed through time. Thus, the mortality of germinating seedlings could be estimated and an idea developed of the phenology of germination (Table 10 and Figure 16).

Overall, 20 percent of the seeds planted did germinate and percent of these germlings survived through the first growing season. The individual species showed a full range of response in both germination and survival. Magnolia was

Table 9. Seed germination in Gardinier seed plots as measured by seedling counts in March and October 1984 along with the total cumulative germination. Data given by species and treatment.

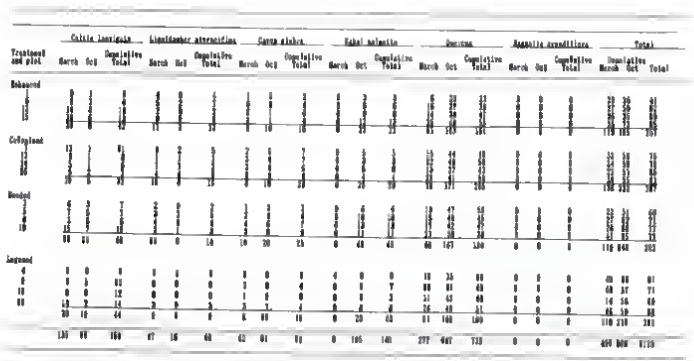
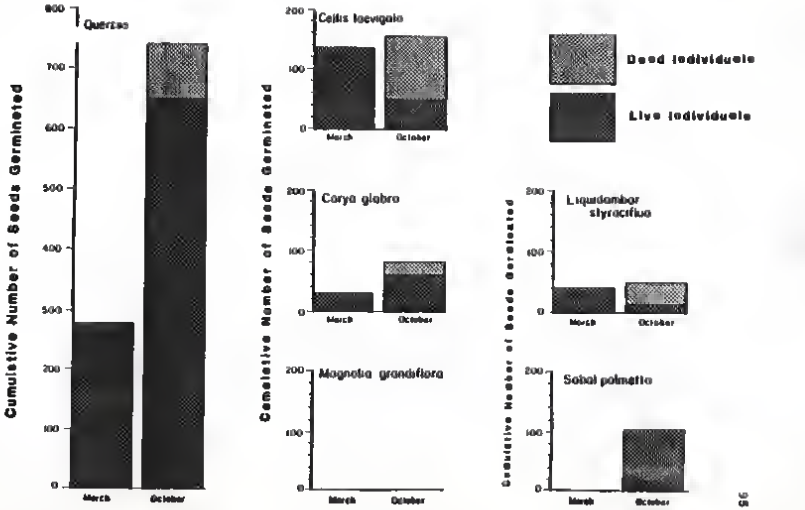


Table 10. Summary of germination and survival results from Gardinier seed plots. The percentage survival is here defined as the percentage of all seeds that germinated which survive to the end of the growing season.

Treatment	Celtis				Liquidambar				Carya				Sabal				Magnolia				Quercus				Total			
	Cumulative germination		Survival		Cumulative germination		Survival		Cumulative germination		Survival		Cumulative germination		Survival		Cumulative germination		Survival		Cumulative germination		Survival		Cumulative germination		Survival	
	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)	n	(%)
[illegible]	33	[illegible]	6	[illegible]	[illegible]	[illegible]	6	(15)	13	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	33	[illegible]	1		1		164	(41)	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]
Colonized	32	[illegible]	1	[illegible]	16	[illegible]	0	[illegible]	[illegible]	[illegible]	10	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	6		6		205	(41)	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]
Seeded	36	[illegible]	21	[illegible]	[illegible]	[illegible]	0	[illegible]	35	[illegible]	[illegible]	[illegible]	36	[illegible]	36	[illegible]	0		6		100	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]
Legumed	[illegible]	[illegible]	[illegible]	[illegible]	6	[illegible]	1	[illegible]	10	[illegible]	10	(72)	35	[illegible]	21	[illegible]	0		0		100	[illegible]	136	[illegible]	[illegible]		[illegible]	[illegible]
	[illegible]	(15)	43	[illegible]	35	[illegible]	16	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	136	[illegible]	105	[illegible]	0		1		740	(49)	640	[illegible]	[illegible]		[illegible]	[illegible]

Figure 16. Number of germinated seeds on tree species planted at Gardinier plots. Seeds planted in fall of 1983 and plots sampled in spring and fall of 1984.


Cumulative Number of Seeds Germinated
Quercus
Celtis laevigata
Carya glabra
Liquidambar styraciflua
Magnolia grandiflora
Sabal palmetto
March
October
Dead individuals
Live individuals

unique in that no seeds germinated regardless of plot or treatment. Sweetgum had only 6 percent germination and only 33 percent of those survived. Sugarberry had 19 percent germination, but only 30 percent survival.

The other three taxa had much higher survival rates. Hickory had 10 percent germination with 75 percent survival. Germination in cabbage palm was 13 percent with 100 percent survival. Oak had both high germination (46 percent) and high survival (87 percent). Because of the difficulty in accurately distinguishing between young laurel oak and young live oak seedlings, the two are treated as a single taxon.

The species showed interesting combinations of germination phenology and survival. The majority of sugarberry and sweetgum germination occurred before the March sampling. Additional seeds germinated between March and October, but mortality in both cases was so high that the total number of live seedlings was lower in October than in March (see Figure 16). Germination of hickory and oak had germination occurred throughout the growing season, with a larger number of seeds germinating after March. For these two taxa, the germination phenology combined with low mortality resulted in a greater number of live seedlings at the second sampling period than the first. Finally, cabbage palm demonstrated a different germination pattern, with all germination occurring after March (see Figure 16).

Another way of analyzing the seed germination and survival data is to compare at the end of season survivors as a proportion of the seeds planted. The data on seedling survival from the experimental plots were converted to percentages for analysis. It is known from statistical theory that proportions or percentages have binomial rather than normal distributions, and that the deviation from normality is greatest for small and large values. The data can be transformed, however, to obtain a distribution that approximates normal. The square root of each percentage was transformed to its arcsine to give an underlying distribution that is nearly normal. The percentages were so transformed (Table 11) before conducting the ANOVA.

For the case where the data are summed over species within each plot the results of two ANOVAs are similar (Table 11a). When data from plots 15 and 18 are neglected in the analysis, the means for the weeded, natural colonizer, and enhanced legume treatments are not significantly different, but the enhanced colonizer treatment mean is lower and significantly different from the other three. When plot 18 is dropped and plot 15 is assigned to the weeded treatment the result is essentially the same.

The plot-by-plot survival results can also be examined for individual species. The analysis assumes that there are no interactions between species. Because this assumption cannot be made for multi-species seed mixes any inferences

Table 11. Comparison of mean percent germination/survival for four experimental treatments (weeded, natural colonizers, legume, enhanced colonizers) using arcsine transformed data. Means compared following an ANOVA, using Duncan's multiple range test. Means with the same letter are not significantly different ($p = .05$).

Table 11a. All species summed

Plot Assignments for ANOVA	PR>F (ANOVA)	Treatment Means: Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected	.0079	25.017 A	23.567 A	22.857 A	19.027 B
Plot 15 Weeded, 18 Neglected	.0031	25.510 A	23.567 A B	22.857 B	19.027 C

Table 11b. Pignut hickory (Carya glabra)

Plot Assignments for ANOVA	PR>F (ANOVA)	Treatment Means			
		Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected		16.080	17.390	14.292	10.897
	NS	A	A	A	A
Plot 15 Weeded, 18 Neglected		16.167	17.390	14.292	10.897
	NS	A	A	A	A

Table 11c. Sugarberry (Celtis laevigata).

Treatment Means

Plot Assignments for ANOVA	PR>F (ANOVA)	Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected	.0772	17.693 A	8.892 A B	12.420 A B	5.847 B
Plot 15 Weeded, 18 Neglected	.0297	18.387 A	8.892 B	12.420 A B	5.847 B

Table 11d. Sweetgum (*Liquidambar styraciflua*)

Plot Assignments for ANOVA	PR>F (ANOVA)	Treatment Means			
		Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected		7.863	11.057	2.992	4.7
	NS	A	A	A	A
Plot 15 Weeded, 18 Neglected		6.217	11.057	2.992	4.7
	NS	A	A	A	A

Table 11e. Oak (*Quercus*)

Plot Assignments for ANOVA	PR>F (ANOVA)	Treatment Means			
		Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected	.0604	42.127 A	41.105 A	39.645 A	33.930 B
Plot 15 Weeded, 18 Neglected	.0347	42.127 A	41.105 A	39.645 A	33.930 B

Table 11f. Cabbage palm (Sabal palmetto).

Plot Assignments for ANOVA	PR>F (ANOVA)	Treatment Means			
		Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected		25.833	18.155	10.410	11.910
	.0841	A	A B	B	B
Plot 15 Weeded, 18 Neglected		27.040	18.155	10.410	11.910
	.0300	A	A B	B	B

regarding the results will lack some degree of statistical rigor. In spite of this inability to meet all assumptions required by theory, the analysis by individual species may provide valuable insight to the hypotheses being tested that might otherwise be ignored. Therefore, an ANOVA was run on the transformed survival data for each species. Magnolia was not included in the analysis because none germinated in any plots. The results are again presented in two ways depending on how plots 15 and 18 were assigned.

Hickory (Table 11b) and sweetgum (Table 11d) are the simplest cases, no significant differences were seen among any of the treatment means in either of the two ways plots 15 and 18 were assigned.

Sugarberry (Table 11c) and oak (laurel oak and live oak summed) (Table 11a) showed similar patterns in response to two different ANOVA situations and both had significant differences in at least some of the treatment means. When plots 15 and 18 were neglected, the two taxa exhibited slightly differing results. For sugarberry, the weeded, enhanced legume, and natural colonizer means were not significantly different, but weeded and enhanced colonizer means were. For oak, the weeded, natural colonizer and enhanced legume means were not significantly different from each other but were all different from the enhanced colonizer mean, which was also lower.

In the second ANOVA configuration, in which plot 15 was assigned to the weeded treatment and plot 18 was ignored, sugarberry and oak showed similar but not identical patterns. The means were not significantly different for sugarberry for the weeded and enhanced legume treatments or among the legume, natural colonizer, and enhanced colonizer treatments. The weeded and enhanced means were different, with the enhanced colonizer value the lower. For oak, the weeded, natural colonizer, and enhanced legume treatment means were not different from each other and all were significantly different from and higher than the enhanced treatment mean.

Cabbage palm exhibited significant differences between some treatment means, but the results were the same for both ANOVA configurations (Table 11f). The means for the weeded and natural colonizer treatments were not significantly different, and the natural colonizer, enhanced colonizer, and enhanced legume means were not significantly different, but the weeded mean was different from and higher than the legume mean.

Height Growth in Seed Plots

Height growth data from the seed plots were analyzed in the same manner as the survival data for each individual species and for the sum of all species (Table 12). When the height data were summed over species, the ANOVA results were the same in both combinations of assigning plots 15 and 18

Table 12. Comparison of mean seedling height growth (cm) for four experimental treatments (weeded, natural colonizers, legume, enhanced colonizers). Means compare following an ANOVA, using Duncan's multiple range test. Means with the same letter are not significantly different ($p \leq .05$).

Table 12a. All species summed

Plot Assignments for ANOVA	PR>F (ANOVA)	Treatment Means			
		Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected	.0001	7.78 A	6.4 B	6.26 B	5.8 B
Plot 15 Weeded, 18 Neglected	.0001	8.02 A	6.4 B	6.26 B	5.8 B

Table 12b. Pignut hickory (Carya glabra)

Plot Assignments for ANOVA	PR>F (ANOVA)	Treatment Means			
		Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected	NS	6.25 A	5.61 A	5.61 A	5.17 A
Plot 15 Weeded, 18 Neglected	NS	5.57 A	5.61 A	5.61 A	5.17 A

Table 12c. Sugarberry (*Celtis laevigata*).

Plot Assignments for ANOVA (ANOVA)	PR>F	Treatment Means			
		Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected		8.5	7.0	6.5	8.0
	NS	A	A	A	A
Plot 15 Weeded, 18 Neglected		8.3	7.0	6.5	8.0
	NS	A	A	A	A

Table 12d. Sweetgum (*Liquidambar styraciflua*)

Plot Assignments for ANOVA	PR>F (ANOVA)	Treatment Means: Weeded	Natural	Enhanced Legume	Colonizers
Plots 15 & 18 Neglected		6.0	5.0	4.0	4.5
	NS	A	A	A	A
Plot 15 Weeded, 18 Neglected		6.0	5.0	4.0	4.5
	NS	A	A	A	A

Table 12e. *Quercus*.

Plot Assignments for ANOVA	PR>F (ANOVA)	Treatment Means: Weeded	Natural	Enhanced: Legume	Enhanced: Colonizers
Plots 15 & 18 Neglected		7.81	6.26	6.19	5.63
	.0011	A	B	B	B
Plot 15 Weeded, 18 Neglected		8.17	6.26	6.19	5.63
	.0001	A	B	B	B

Table 12f. Cabbage palm (Sabal palmetto).

		Treatment Means			
Plots 15 & 18 Neglected	NS	8.14 A	8.65 A	7.09 A	7.67 A
Plot 15 Weeded, 18 Neglected	NS	8.23 A	8.85 A	7.09 A	7.67 A

(Table 12a). In both cases, the F-value was significant ($p = .0001$) and the mean height growth for the weeded treatment was significantly different and higher than the other three treatment means. There were no significant differences among the means for the natural colonizer, enhanced legume, and enhanced colonizer treatments. Assigning the height growth data by individual species reveals an interesting trend. Generally, the oak results mimicked the results from the combined species data, while hickory, sugarberry, sweetgum, cabbage palm, and magnolia all had similar results as a group that were quite different from oak.

As in the case with height data summed over species, the oak data had a highly significant F-value for both ANOVA regimes. The weeded treatment mean was found to be significantly different from and higher than the other three treatment means, which were not significantly different from each other (Table 12e). For the most part, the growth response of the other four species (hickory, sugarberry, sweetgum, and cabbage palm) were similar. In all cases, no statistically significant differences were seen among the treatment means (Tables 12b, 12c, 12d, and 12f).

Height Growth in Transplant Plots

The three species (sweetgum, live oak, and cabbage palm) were first treated separately in the analysis under the assumption that the 1-m spacing between seedlings would

prevent any interaction between species. Analysis was also performed summing growth data for all three species together.

The ANOVA of the height growth data for each of the three species showed a significant F value ($p < .05$) (Table 13), indicating that at least one of the treatment means was significantly different from the rest. Duncan's multiple range test was used to determine which treatment means were significantly different (Table 13).

For sweetgum seedlings, the mean height growth for the weeded treatment was significantly different and higher than the mean height growth of the other three treatments, and there was no significant difference among the means for the natural colonize, enhanced colonizer, and enhanced legume treatments.

The mean height change for the live oak seedlings was also significantly different for the weeded treatment. The live oak seedlings in the weeded plots had a higher mean growth change over the first growing season. The analysis again showed no significant difference among means in the other three treatments.

The Duncan's multiple range test for the cabbage palm data yielded different results. Weeded, enhanced legume, and natural colonizer treatments were not significantly different from each other and neither were the natural and enhanced colonizer treatments. The weeded and legume treatment means

were both significantly different from and higher than the enhanced treatment mean.

When growth data were summed over species, the results were the same as for sweetgum and live oak. The mean for the weeded treatment was significantly different and higher than the means for the other three treatments, which were not significantly different from each other.

Mound-Building Ants

Mound Survey

The field surveys showed mound densities of 560/ha, 2,070/ha, and 2,100/ha for the 1-, 2-, and 5-year old sites, respectively. Average mound volumes were 600 cm^3, 2,420 cm^3, and 1,250 cm^3 for the 1-, 2-, and 5-year old sites, respectively.

Plant Growth Study

The results of the assay grass growth test (Table 14) show a uniform trend of significantly different and higher growth rates for the plants grown on mound soil for all three sites. A statistically significant growth enhancement was found in all three cases for the aboveground, belowground, and total plant biomass. For all comparisons, the mean biomass value for the mound samples was higher and significantly different ($P \leq .01$).

Table 14. Results of vasey grass growth bioassay on mound and non-mound soils from 1-, 2-, and 5-year old sites.

Site (age)	Seedling Growth Parameter	Mean Mound Soil	Non-mound Soil	P
Tiger Bay (1 year)	Below ground biomass (g)	0.242	0.139	.002
	Above ground biomass (g)	0.386	0.162	.0005
	Total biomass (g)	0.626	0.301	.0006
Fort Green (2 year)	Below ground biomass (g)	0.233	0.145	.0003
	Above ground biomass (g)	0.226	0.153	.004
	Total biomass (g)	0.459	0.296	.0004
Clearsprings (5 year)	Below ground biomass (g)	0.264	0.172	.0001
	Above ground biomass (g)	0.308	0.160	.0003
	Total biomass (g)	0.592	0.332	.0001

The sweetgum growth bioassay also showed a uniform growth enhancement on the mound soil (Table 15). For all growth parameters measured (stem biomass, root biomass, leaf biomass, total biomass, leaf area, and stem height), the mean for the mound soil was significantly different ($P \leq .05$) and higher than the non-mound mean. For biomass and leaf area growth parameters, the means for the seedlings grown on the three mound soils were at least twice those of the seedlings on the non-mound soils.

Chemical Soil Analyses

Chemical analysis of mound and non-mound soils highlights some differences in several of the chemical parameters assayed. Because the sampling technique used was paired samples, results are presented as mean differences of each pair with the non-mound value subtracted from the mound value (Table 16). Positive differences connote higher values for the mound samples.

pH values exhibited a wide range at each of the three sites but tended to be circumneutral as compared to the characteristically acid soils native to the region. The mean difference of pH values between pairs was not statistically different at any of the three sites.

Calcium levels showed no statistically significant differences between sample pairs from any of the three sites. For magnesium and manganese, no statistically significant

Table 15. Results of sweetgum growth bioassay on mound and non-mound soil from 1-year old site.

Seedling Growth Parameter	Mean for mound soil (n=5)	Mean for non-mound soil (n=6)	P
Stem biomass (g)	0.41	0.14	.0001
Root biomass (g)	0.99	0.42	.0002
Leaf biomass (g)	0.34	0.17	.0003
Total biomass (g)	1.73	0.67	.0001
Leaf area (cm^2)	89.66	44.30	.0003
Stem height (cm)	13.4	9.68	<.03

Table 16. Results of paired-difference comparisons between mound and non-mound soils for selected chemical parameters from Tiger Bay (1 year-old), Fort Green (2 year-old) and Clearspringe (5 year-old) reclamation areas.

		Difference (Mound - Non-mound)			
	Site Age (Years)	Mean	Error	Range	P
Calcium (mg/k)	1	115.0	227.4	-250 to 1150	NS
	2	-158.5	341.5	-1370 to 570	NS
	5	-91.3	388.7	-510 to 140	NS
Magnesium (mg/k)	1	108.3	121.8	-98 to 700	NS
	2	-38.3	51.4	-288 to 50	NS
	5	48.3	15.1	-10 to 100	.08
Manganese (mg/k)	1	1.2	0.75	0.0 to 5.0	NS
	2	0.0	0.20	-1.0 to 1.0	NS
	5	1.5	0.5	2.0 to 5.0	.01
Potassium (mg/k)	1	94.2	25.8	37 to 168	.05
	2	55.5	5.9	26 to 84	.01
	5	79.3	14.5	52 to 141	.01
Sodium (mg/k)	1	28.3	10.7	8 to 72	.01
	2	24.0	5.3	4 to 54	.01
	5	7.0	2.0	0 to 14	.05
Nitrogen (mg/k)	1	1903	180	1280 to 3220	.01
	2	784	188	150 to 1979	.01
	5	1363	170	210 to 2730	.01
Organic Matter (%)	1	0.51	0.18	-.06 to 1.37	.08
	2	0.27	0.15	-.30 to 0.88	.2
	5	0.15	0.08	-.13 to 0.52	.2
pH	1	0.73	1.212	-26 to 1.50	NS
	2	-0.33	1.320	-.83 to 0.56	NS
	5	0.11	0.561	-.21 to 1.12	NS

differences were seen between sample pairs for the 1-year old and the 2-year old sites, but a significant positive difference was reported for the 5-year old Clearspring site. Magnesium values were an average of 49.3 g/kg higher in mound soils than in non-mound soils. Manganese values were 2.5 g/kg higher in the mound soils.

Potassium and sodium each had a statistically significant and positive difference at each of the three sites. For potassium, the mean difference was 94.5 g/kg for the 1-year Tiger Bay site, 55.5 g/kg for the 2-year site, and 79.3 g/kg for the 5-year site. The mean difference for sodium was 29.3 g/kg for 1-year site, 24.9 g/kg for 2-year site and 7.0 g/kg for 5-year site.

Nitrogen values followed the same pattern as potassium and sodium with statistically significant ($P \leq .01$) positive differences at all three sites. Mean differences for the mound and non-mound soils were 1,902, 764, and 1,943 g/kg for the 1-, 2-, and 5-year sites, respectively. Tiger Bay mound samples had a range of nitrogen levels from 2,429 to 4,039 g/kg as compared to 539 to 2,709 g/kg for the non-mound soils. At the 2-year old Fort Green site, the ranges were 2,450 to 3,325 g/kg and 1,995 to 2,970 g/kg for the mound and non-mound samples, respectively. For the 5-year old Clearspringe site, the ranges were 3,999 to 6,999 g/kg for the mound soils and 1,869 to 5,089 g/kg for the non-mound soils.

The organic matter analysis was less determinate but indicated some of the same trends. At the 1-year old Tiger Bay site, the mean difference for soil organic matter was significantly different ($P \leq 0.5$) and positive. Positive differences were also shown for 2-year old Fort Green site (27 percent) and the 5-year old Clearsprings site (15 percent), but these differences were only significant at marginal levels ($P \leq .20$)

Physical Soil Analyses

Bulk density. Bulk density measurements (Table 17) on soils from the one site that was sampled, the 2-year old Fort Green site, showed a statistically significant difference between the means for the mound and non-mound samples. The mean bulk density of the mound samples was 1.19 g/cm^3, compared to 1.74 g/cm^3 for the non-mound samples.

Mound volumes can be calculated from circumference and height measurements, assuming a conical mound shape. Volumes range from 50 to 2850 cm^3. Based on a average bulk density of 1.2 g/cm^3, a mound of average volume (approximately 1250 cm^3) has a soil mass of approximately 1,500 g.

Infiltration Tests. Results of the three water infiltration tests at the Fort Green site (Table 18) showed the infiltration rate on mound soils to be considerably higher than on the adjacent non-mound soils. Mound soil infiltration

rates were 5, 17, and 120 times higher than rates on the adjacent non-mound soils for tests 1, 2, and 3, respectively. Mound soils had infiltration rates of 0.1 to 6.0 cm/min versus 0.02 to 0.05 for the non-mound soils.

Table 17. Results of bulk density analysis of mound and non-mound soils from 2-year old site (n=7).

	Standard Mean	Error	Range	P
Mound	1.19 g/cm^3	0.0735	1.00 to 1.43	.05
Non-mound	1.74 g/cm^3	0.0473	1.66 to 1.99	

Table 18. Results of water infiltration tests on mound and non-mound soils at the Fort Green reclamation area.

	Soil Type		Infiltration Rate
Test #1	Mound	11 cm/120 minutes	(0.09 cm/min)
	Non-mound (grass)	2 cm/120 minutes	(0.017 cm/min)
	Non-mound (algal mat)	1.5 cm/120 minutes	(0.012 cm/min)
Test #2	Mound	26 cm/60 minutes	(0.43 cm/min)
	Non-mound (grass)	1.5 cm/60 minutes	(0.025 cm/min)
Test #3	Mound	>120 cm/20 minutes	(>6.0 cm/min)
	Non-mound (grass)	1 cm/20 minutes	(0.05 cm/min)

DISCUSSION

Marsh Development

Seed Bank Formation

The formation of a seed bank appears to be a relatively rapid process, beginning almost immediately after the land surface has been exposed. Seed bank samples from all but the youngest mine sites fall within or just below the range of seed density and species diversity found in natural wetlands in Florida, Iowa, and New Jersey.

The species present in the seed bank samples are largely the wetland ruderal species characteristic of environments subject to disturbances such as water level fluctuations. They are the initial colonizing species, the annuals and short-lived perennials of exposed mudflats, wetland transition zones, and shallow littoral zones. Notably absent are the late successional marsh species: the emergent macrophytes, submergent macrophytes, and free-floating aquatic species. A possible reason is the germination conditions used in the seed bank tests, which were similar to those of an exposed mudflat, but the absence of the seeds of the late successional species from the samples is a more likely cause. The seeds

and fruiting bodies of many macrophytes (pickerelweed, water hyacinth, cow-lily (Nuphar luteum), white water-lily (Nymphaea odorata), Sagittaria, and Peltandra virginica are large enough to be easily seen, and no large seeds were observed in any of the samples.

The question arises of how pickerelweed, Sagittaria, cow-lily, and white water-lily could be present in at least a few of the wetlands sampled, if none of their seeds were detected in this assay. It may be beneficial to discuss the species present in the seed bank samples versus those conspicuous by their absence in terms of successional status and life history characteristics of the adult, established phase and juvenile, regenerative phase. Regenerative strategies may be related to successional status.

Formation of a persistent seed bank represents only one of three regenerative strategies used by wetland plants; the others are vegetative expansion and production of numerous wind-dispersed seeds. Generally, vegetative expansion, is successful where the adult plant is already established. Most long-lived macrophytes are capable of vegetative expansion which allows for rapid colonization of open space, such as small patch disturbances within a large existing stand of marsh vegetation. In habitats characterized by chronic but unpredictable disturbance (fire, flood, or drought), where vegetative structure is destroyed over large areas, the persistent seed bank is typically the primary regenerative

mechanism. The third regenerative strategy employed by wetland plants, the production of numerous wind-dispersed seeds, is useful in colonizing near and distant open areas, especially those that lack a seed bank.

Many species employ more than one strategy. Seeds of most wind-dispersed species remain viable at least for short periods of time in a seed bank. Cattail uses all three regenerative strategies; it is capable of rapid vegetative growth and produces prodigious amounts of wind-dispersed seeds, which are also capable of lying dormant in a seed bank.

The perennial macrophytes present within the wetland zones sampled may rely on vegetative expansion as their primary regenerative strategy. Alternatively, their seeds may have been present but in relatively scarce amounts or a patchy distribution. As noted earlier, all root and rhizome material was removed from the samples. In hindsight, it would have been instructive to retain the root/rhizome material and check for sprouting.

Even for species that use vegetative expansion as the primary regenerative strategy, the production of viable seed represents an essential component of the total regenerative strategy.

Formation and Stability of Macrophyte Communities

In regard to the pattern of succession observed at the Fort Green marsh, the vegetation dynamics described in this

study show that the plant communities that developed in the two treatment areas differed in species composition and that these differences remained stable through at least the first four growing seasons. This stability suggests that initially established vegetation can occupy the available open space and resist invasion or encroachment by other taxa. Dense stands of pickerelweed established in the muck treatment areas remained stable and were not invaded by cattail, primrose willow, or other aggressive weedy species typically associated with arrested succession on unreclaimed phosphate-mined lands. Similarly, dense stands of cattail have also remained stable, resisting invasion. In contrast, open stands of cattail in other portions of the wetland were invaded by bulrush in 1984 and 1985. Recent studies show that dense stands of bulrush have since developed in these areas, competitively displacing the cattail (G.R. Best, personal communication, 1988). Bulrush showed an ability for widespread dispersal of waterborne seeds, colonization, and rapid vegetative expansion.

The marsh transect studies indicated that the initial floristic composition, sensu Egler, largely determined the species composition within the marsh, and that in the absence of disturbance, the initial vegetation pattern and species composition are maintained for some time, possibly even long-term.

Patch dynamics. The use of permanent transects allowed the fate of individual patches to be tracked through time. The large stands of cattail and pickerelweed developed from individual plants or patches that gradually coalesced into larger units. A similar pattern of plant establishment can occur on abandoned coal-mined land, as patches or islands that grew individually and eventually coalesced (Game et al., 1982). Some patches disappear and are replaced by an individual or group of individuals of another species. This suggests that a patch has to be of some critical size before it can be successfully established, and that the "critical" patch size probably changes as a function of the surrounding vegetation and the growth rate of the species.

The vegetation pattern composition and species composition of a marsh community appear to be largely a function of the propagules available and the prevailing environmental conditions which supports the seed bank/environmental filter model described by van der Valk (1981). The community responds to an array of environmental factors that effect its composition. Major environmental factors affecting wetland communities include depth, duration, and seasonal pattern of flooding, and fire.

Effect of Herbivory. Herbivory can also be an important factor regulating species composition and productivity in wetlands. Feral hogs are common in the Payne Creek floodplain

and create patch disturbances of varying size within the wetland. The affected areas are typically disturbed down to the subsoil, with all vegetation removed. The hog activity observed during the marsh study was generally restricted to the wetland/upland transition zone. Bersok (1986) found the impact of the foraging hogs in this marsh was limited to monospecific stands of cattail, and patches opened by hogs were recolonized by vegetative expansion of the surrounding cattail plants. This type of disturbance may be similar, although less extensive, to the muskrat "eatouts" described by van der Valk and Davis (1976) and Weller (1981) in marshes in the midwest. The effect is to create a shifting mosaic of open areas available for colonization.

Effect of Hydroperiod and Drought. The hydroperiod factors of depth, duration and seasonal pattern of flooding have a broader impact than hog activity on the marsh. The water level fluctuations provide a seasonal dynamic. Of more importance though are the events with periods longer than a year, such as the regional drought cycle that occurred from fall 1984 through summer 1985.

As the drought cycle is a natural part of the climatic regime, it is one to which a wetland must be adapted. The reaction to the 1984-85 drought showed that the marsh had developed a mechanism to respond to environmental change. Drought conditions exposed previously flooded but unvegetated

areas that were colonized subsequently and rapidly by a variety of species. The timing of the drought and the species composition on the exposed flats demonstrated that the source of the colonizing species was the seed bank. The wetland had developed its own seed bank, which is one of the principal response mechanisms of wetlands to wide fluctuations in water level.

Mature wetland systems respond to change with an *in situ* mechanism that includes the seedbank as a major component. In a short period, the Fort Green wetland has developed its own seed bank. The muck applied in 1982 provided an instant seed bank to certain areas, but the vegetation dynamics highlighted during the drought occurred in areas where no muck had been applied. Even on the muck treatment transects (97, 105, and 139) the rise of dogfennel and bulrush was confined to those portions that had not received the muck treatment.

The establishment of bulrush and *Sagittaria* on drought-exposed flats at the north end of the site is particularly interesting, as the propagule source was undoubtedly from within the wetland itself, and highlights the autogenic aspect of community development in seedbank formation. Bulrush and *Sagittaria* were planted; initially established plants spread vegetatively, produced seed, and now act as seed sources for further colonization. The formation of an internally generated seed bank may be one indicator of ecosystem maturity.

Monitoring the fate of the drought-stressed or drought-killed macrophyte communities will provide some additional insight into community dynamics in future years. Major patches of cattail and pickerelweed senesced in response to the drought (Figures 15e through 15f). Only time will indicate whether the whole plant was killed or only the aboveground portions. If the latter is the case, then the drought may have only hastened the annual fall senescence, as the aboveground portions of both taxa annually die back and the plants overwinter as leafless rhizomes. Even if large patches were killed by the drought, species replacement may be slowed or inhibited by the presence of standing dead plant tissue; since as these studies have shown, an occupied space is difficult to colonize.

The marsh transect study does not and cannot address the long-term stability of created marsh communities like Fort Green site. There is no reason to believe that the marsh system will not eventually develop into a forested wetland. Tree seedlings planted within the wetland have done quite well through the first four growing seasons (Best and Erwin, 1984; Erwin et al., 1985). The mature marsh system may actually be an immature swamp system.

Wetland Succession Model

Role of Life History Characteristics

Regenerative strategies and other life history characteristics are the foundation of van der Valk's wetland succession model. The plant community's response to climatic cycles of flood and drought and changing environmental conditions is analyzed through the life history characteristics of the species residing in the seed bank. The environmental factors in the model act as a "sieve" and screen species from the seed bank. The life history characteristics considered in the model include: propagule longevity (short-lived dispersing or long-lived seed bank forming), life span of the established plant (annual or perennial), and propagule establishment requirements (germination under drawdown or flooded conditions). The model has generally been applied to succession in marsh systems, but would seem to be equally appropriate for forested wetlands. The addition of woody species could be easily accomplished by incorporating the appropriate life history characteristics for propagule longevity, propagule establishment requirements, and life span of the established plant.

Importance of Allogenic and Autogenic Factors

The van der Valk model is useful in describing some aspects of wetland succession and showing the importance of

allogenic forces (the environmental sieve) on the wetland vegetation. The model emphasizes, as did Gleason and others (Drury and Nisbet, 1973; White, 1979), that the key to vegetation dynamics lies in understanding the life history characteristics of the species constituting the vegetation. This suggests that succession can be explained entirely as a disintegrated individualistic phenomenon.

A conceptual model with a focus limited to allogenic factors and the life history strategies of the individual species ignores many of the biological properties of the wetland community. The model's focus on secondary succession assumes that the community structure is already in place and does not account for the processes that build that structure. The model does not explicitly recognize the autogenic processes and, therefore, lacks the feedback to show how the environmental sieve can itself be modified to some extent by the wetland vegetation.

An example of autogenic feedback is the formation of an organic soil through peat deposition. Wetland succession can occur on mineral soil, depending on the site conditions and the nature of the disturbance that initiated the succession. Certainly, in the case of unreclaimed mined land, the wetland community will develop on mineral substrate. Through time, an organic substrate accumulates as litterfall exceeds decomposition. The accumulated organic sediments raise the effective ground level in the wetland, thus altering the

effects of changes in depth frequency and duration of flooding. The organic sediments also provide a rooting medium, seed storage medium, and microfaunal habitat that is quite different from the underlying mineral substrate.

The model fails to recognize that wetlands tend to change with time from "young" to "older," more mature stages (Mitch and Gosselink, 1986). Young stages after establishment are characterized by (1) plant species that are opportunistic, early colonizers capable of being established from seed and growing in a variety of different habitats, (2) soils that are typically mineral in nature with low organic matter content, and (3) subsurface hydrology and chemistry controlled by the mineral soil. As the system ages, it becomes more "mature": (1) the plant community may become dominated by species more characteristic of mature wetland systems, (2) the wetland soils may gradually change and gain an increasing amount of organic matter, and (3) the subsurface hydrology and chemistry may change in response to the changes in wetland soils.

Maturation is to a large extent the action of the autogenic processes within the wetland. The accumulation of sediments and the formation of an organic soil is due to litter production, decomposition, and the depth and duration of flooding. By building the soil structure, the biological community provides a feedback to the environmental sieve and modifies its effects. The mature community has a greater degree of internal control than the young community.

Another example of the process is found with cypress domes which may influence the shape and depth of their own basins through the production of acid waters, that percolate down and cause solution of the underlying limestone (Odum, 1984). Also, the sawgrass marshes of the Florida Everglades are fire-adapted communities whose continued survival depends upon fire (Wade et al., 1980). The sawgrass plants accumulate fuel in the form of standing-dead leaf litter, and when sufficient litter has accumulated and conditions are right, a fire may occur. Fire is an allogenic process, but the timing, frequency, and severity of the fire are influenced by the growth characteristics of the sawgrass.

Another excellent example of this kind of feedback loop is discussed by Weller (1981). In midwestern prairie pothole marshes, the vegetation is periodically destroyed by muskrats. New emergent vegetation cannot become established until a dry year exposes the substrate. A typical succession follows until cattails out-compete the other plant species. This sets the stage for another muskrat population explosion. The cycle has a 5- to 8-year frequency that depends on both the biotic vegetation-muskrat interaction and the abiotic water level-climate cycle.

Eclectic Wetland Succession Paradigm

Evidence supports the conclusion that both allogenic and autogenic forces act to change wetland vegetation. A paradigm

or conceptual model of wetland succession must recognize both these forces and the interplay or feedback between them. An alternative formulation of the van der Valk model (Figure 16) can be developed to include other system components, such as the wetland substrate and consumers, and to show the feedback relationships between the components and the environmental sieve.

With regard to the competing paradigms (initial floristics, inhibition, relay floristics, coevolution, and self-organization), this work and other studies indicate that all are operating at some time during wetland succession. The formation of plant communities from seed/propagule banks following disturbance is a case of initial floristics. Bersok (1986) found no significant difference between tree seedling success in cleared plots versus cattail plots. Pickerelweed and cattail stands that remain stable in the absence of disturbance and support to the inhibition model. Coevolution and relay floristics are important in wetland tree dispersal; bird and mammal species involved in seed dispersal must have their habitat requirements satisfied before they will use the site. Seed/propagule banks and accumulated belowground structures (e.g., roots, rhizomes) provide a storage of "choices" for all environmental contingencies, thus supporting the self-organization model.

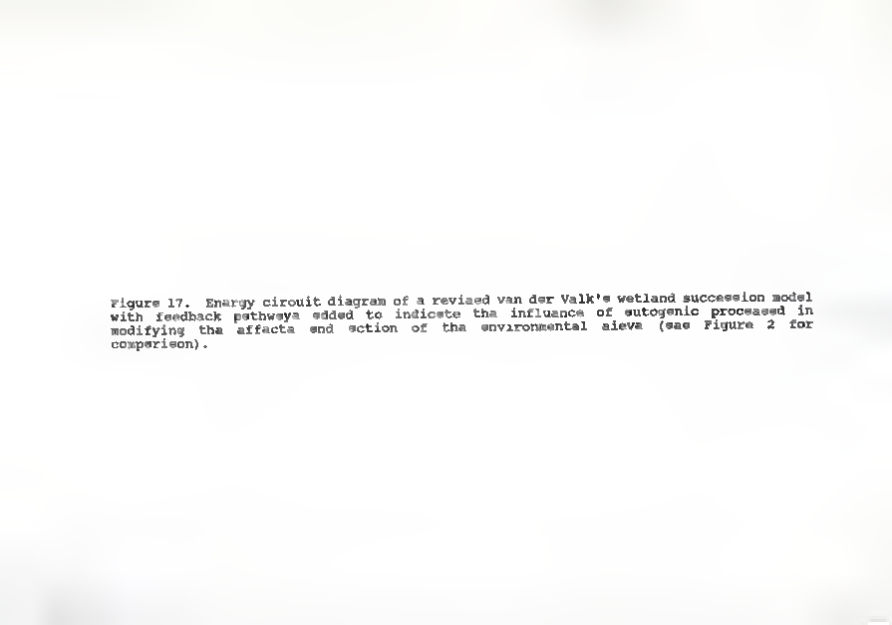


Figure 17. Energy circuit diagram of a revised van der Valk's wetland succession model with feedback pathways added to indicate the influence of autogenic processes in modifying the effects and action of the environmental sieve (see Figure 2 for comparison).

Actual Goal
Emergent Goal
Apparent Goal
Environmental Conditions
Environmental "Sieve"
Actual
Emergent
Apparent
Sentient Self Elder
Mud Flat Animals
Emergents
Apparents
Sun

Upland Forest Plots

Seed Germination and Survival

The germination results and accompanying survival rates for the seed highlight several points. First, germination rates between species differ widely under field conditions, as shown by the two extremes of magnolia with no seeds germinating and oaks with nearly 100 percent germination. Germination was low for hickory, sugarberry, sweetgum and cabbage palm. Factors apparently affecting germination success include seed quality, site condition, seed predation, and seed size. The survival of individuals that germinated exhibited interesting species-specific trends that appear related to seed size and seedling adaptations.

Effect of Seed Quality. Sugarberry, sweetgum, hickory, cabbage palm, and magnolia seeds had been collected a year before the study and stored dry at 4°C; oak acorns were collected the month before planting and stored outside in potting soil. The storage regime, as well as the initial quality of the seed, could have had an effect on germination potential. Many of the acorns were nearly germinating when planted. Also, because germination was determined only from the two sampling periods in March and October, any seeds that germinated but survived only a short time for would have been overlooked. This factor would have been more critical for

sugarberry and sweetgum, since these species produce a rather delicate seedling.

Effect of site conditions. Seeds respond to environmental cues to germinate. In some cases, dormancy must be overcome. It is possible that the conditions in the field plots were more generally suited for some species than others.

Effect of seed predation. Losses of seed and young seedlings could also bias the germination results. Seed losses to birds and small mammals are always a danger to any direct-seeding operation and are one of the primary causes of low germination in natural conditions, but for large-seeded species, this is also a necessary cost of dispersal. Freshly disturbed soil often attracts animals that consume seeds as part of their diet. Armadillos were observed on the study plots and raccoons, field mice, and feral hogs were also present in the reclamation area.

Two factors were observed to lower the germination potential of hickory, one physical and the other biological. The hickory nut is very large and was easily winnowed out of the soil during heavy rain. This process may have been aided by the removal of hickory nuts by armadillos. Tracks and signs of soil disturbance in the plots by these animals were seen on several occasions, and the signs were usually associated with the presence of only the outer husks of the hickory nut.

No other seed predators were ever in evidence, although the freshly disturbed and seeded plots could have attracted birds and small mammals alike. Seed loss from predation is a process occurring regularly in natural systems.

Effect of Seed Size. The germination and survivel data (see Tables 9 and 10) highlighted some differences concerning seed size and seedling growth form. The species used in the seed plots fall into three categories based on seed size: Sweetgum has a small winged seed adapted for wind dispersal, and the small seed contains little food to nourish a young seedling after germination. Both sugarberry and cabbage pale have intermediate-sized seeds. The seeds have a fleshy exocarp to attract birds and mammals as dispersal agents, and both have modified cotyledons for food storage. Hickory, laurel oak, and live oak produce large, heavy seeds that obviously do not disperse far on their own. These species are highly dependent on animals for that function. Acorns and hickory nuts have large, starchy cotyledons that provide nourishment to the developing seedling, as well as to potential seed predators.

The relationship between the food reserve of modified cotyledons and the survival rate of a germinated seed is striking. The large-seeded species had high rates of survival; 75 percent of all germinating hickories and 87 percent of all oaks survived. In contrast, only 33 percent of the sweetgum individuals survived the first growing season.

In the intermediate seed-size group, sugarberry had low survival while cabbage palm had the highest possible survival.

The cabbage palm results may be anomalous, both because of the phenology of this species and the sampling schedule. During the first sampling period in March, no cabbage palm seedlings were present on any of the plots. All cabbage palm seedlings present in the October census had germinated between late spring and summer. Under this schedule cabbage palm seedlings had 100 percent survival. This could be misleading, because the cabbage palm seedling has a single, short, very leathery leaf, that resists decay for some time, even if dead. If cabbage palm seeds had germinated and the seedling later succumbed, the leaf could have remained long enough to be counted in the survey. Because there is no evidence to support this possibility, it is assumed that there may have been some slight mortality, but that survival rates for cabbage palm were high.

The relatively superior performance of large-seeded species in direct-seeding trials has been noted in other studies. Toumey and Korstian (1942) noted that seeds containing a large amount of reserve food and germinating in early spring are better adapted for direct seeding than small seeds that are slow to germinate and produce plants of slow juvenile growth. Taskett and Grimes (1983) seeded three large-seeded species (Quercus rubra, Q. palustris, and Q. macrocarpa) with two small-seeded species (Paulownia tomentosa

and Alnus glutinosa) and found that after 5 years, a greater number of oak seedlings were established than seedlings of the small-seeded species.

Seedling Adaptations to Drought Stress. Seedling growth form can be especially important in determining the fate of germinating seeds. Along with its tough, leathery leaf, the cabbage palm seedling possesses a thick, leathery root system and is well adapted to handling drought stress. The aboveground and belowground tissues are strong enough not to collapse under moisture tension. Conversely,the sugarberry seedling has a delicate stem and root that are more rapidly affected by moisture stress. It is thus reasonable to assume that sugarberry mortality would be higher than that of cabbage palm if dessication were a problem, as is the case on exposed, unvegetated, overburden soils.

This analysis of seedling anatomy can be extended to the other taxa in the study. Sweetgum, like sugarberry, produces a seedling with delicate shoot and root and would be expected to be killed more easily by drought stress. Hickory and oak both produce a stout woody shoot and a tough fibrous root system that makes them better adapted for coping with water stress.

The survival data for all species summed together showed that the enhanced colonizer treatment had the lowest values. Several factors may have influenced this outcome. Competition

among tree seedlings and herbaceous plants may have been more intense in the enhanced treatment plots, thus reducing survival and possibly germination. Allelopathic inhibition of either growth or germination of woody plants by the species added is also possible. One of the enhanced colonizers, Andropogon virginicus, has been reputed to produce allelochemicals that inhibit the growth of other plant species (Rice, 1978).

Effect of Erosion When the major erosion problems began in early January 1984, the extent and degree of erosion on site were assessed and mapped. An examination of the map and field notes from this time show that eight seed plots were affected by erosion rills. By chance, the affected plots were evenly distributed among the four treatments. Several plots affected by erosion exhibited low survival and others showed high values. Only in two cases were seeds observed to have been washed out of plots (numbers 12 and 13) and these were replaced by hand. However, this does not preclude the possibility of some seeds having been lost completely from some plots or washed from one plot into a down-slope plot. One indication that there was no significant movement of seed between plots is that no individuals of any of the planted legume species were ever found in plots other than the ones in which they were placed.

The germination and survival results for the individual species were varied and less clear in support of one of the

three models. Hickory and sweetgum exhibited no significant differences in survival under any of the four treatments, which provides support for the initial floristics model. The results may be influenced by the generally very low survival values, as some plots had only a single individual or none at all.

Germination and survival results for sugarberry do not clearly favor any of the three models, and also may have been effected by generally low numbers of seeds germinating and surviving (less than 6 percent overall).

Cabbage palm germination results appear to reject the relay floristics model but do not clearly favor either initial floristics or inhibition. The weeded mean was higher than the means for the two enhanced colonizer treatments (legumes and old-field weeds), but the mean was not different from the colonized treatment where the treatment seeds were added naturally.

The results for oak also do not clearly support any of the three models, although there is some support for rejecting the relay floristics model. The weeded, natural colonizer, and enhanced legume means were significantly different from and higher than the enhanced colonizer mean, but the three means were not different from each other. Once again, the enhanced treatment came out lowest, raising the question of whether competition, allelopathy, or another form of inhibition was involved because of the species added in this

treatment. The means for the other three treatments were not significantly different. The oak results may be similar to those of hickory, suggesting a causal relationship between large food reserves in the seed and less treatment-related mortality in the first growing season.

Height Growth

Seed plots: When seedling height data are summed for all species, significantly different and greater height growth appear to be a result of the weeding treatment. This result seems clearcut and profound, as seedlings in the multi-species plots grew significantly better under the weeding treatment, and relay floristics and initial floristics models must therefore be rejected in favor of the inhibition model. Closer examination, however, indicates the results may actually support more than one model.

When the growth data are summed over all species, the resultant data set is heavily biased toward the oak; both because the two oak species were combined to avoid skewing results from misidentification of individual seedlings and because oak had a higher level of germination and survival than the other taxa. Oak seedlings made up 74 percent of all seedlings found, whereas cabbage palm comprised 12 percent, hickory 7 percent, and sugarberry and sweetgum 5 and 2 percent, respectively. It is therefore not surprising that the height growth analysis for oak has exactly the same

results as the analysis for all species summed. The vastly greater number of oak seedlings masks the responses of the other species, which, if examined seperately or at least apart from the oak data, lead to a much different conclusion.

The results of the height growth analysis for the other four species are surprisingly uniform and contradictory to the oak results. The ANOVAs for each show no significant differences in mean seedling height among any of the four treatment means, which supports rejection of the relay floristics and inhibition models in favor of the initial floristics model. This may indicate that individual species do not show the same response.

In addition, the erosion problems encountered early in the study provide support for the relay floristics model, by showing that the early colonizing plants help stabilize soil.

Transplant plots. The transplant plot seedling growth data can be considered to provide either clarity or more confusion. Unlike the seed plot data, the transplant plots did not have differing interpretations depending on whether species were combined or treated separataly. The result were the same for three cases and barely dissimilar for the fourth case. For sweetgum, oak, and all species combined only the weeded treatment was shown to be significantly different and it had the highest height growth. For cabbage palm, the mean seedling growth in the weeded treatment was not clearly

superior but it was, along with the natural colonizer treatment, significantly different from and higher than the enhanced legume treatment mean.

Comparisons between seed and transplant plots. The seedling height growth results from the seed and seedling plots provide two views of the interaction between later-arriving tree species and colonizing plants. Because the three species used in the seedling transplant plots were also in the seed plots, a valuable means of comparison was provided.

The oak seedlings exhibited the same height growth response under experimental treatments in both the direct-seeded and transplant plots. The increased height growth under weeded conditions was common to both, as well as for all species combined. These two cases provide some support for the inhibition model, the oak bias in the seed plots must be considered when all species are combined.

Sweetgum demonstrated an interesting contradiction in response to treatments from the seed and transplant experiments. Growth data from the seed plots favored the initial floristics model, as none of the treatment means were significantly different. In the transplant plots, however, sweetgum growth was best in the weeded treatment, thus favoring the inhibition model. The results indicate another variable to consider; that is, that species may have different life history stages that respond differently to early colonizing species. If this is true, then the question of

addressing the pattern and process of ecosystem development becomes inextricably more complicated. However, the very low levels of germination/survival of sweetgum in the seed plots caution against giving strong support to the results.

Like sweetgum, cabbage palm also showed an opposite response to treatment effects from the seed and transplant plots. The seed plot data favored the acceptance of the initial floristics model, while the transplant plot results were not clearly weighed toward either the inhibition or relay floristics models.

The two experiments can be seen to address the same fundamental issues of earliest succession at two succeeding stages of development. The direct-seeded plots simulated the critical period during the first growing season after propagules arrive at an open, uncolonized landscape. The proper cues must be made for germination, establishment depends on a suitable microenvironment, and adequate resources must be continually available for survival. The transplant plots mimicked the second growing season, the next stage in woody plant life, which is less precarious than germination and establishment but still heavily dependant on the quality of the microenvironment. The results of the experiments are strikingly similar for these two stages; in no case was germination or growth (as measured by height change) enhanced or increased by the presence of the natural or enhanced colonizer treatments. The results appear to offer strong

support for questioning the validity of the initial floristics and especially the relay floristics paradigms.

It is somewhat surprising that the height growth results most strongly reject the relay floristics paradigm, as it was assumed at the outset to be important during the early stages of primary succession on phosphate-mined lands. Unvegetated overburden soils provide seeds and seedlings little amelioration or insulation from extreme physical conditions such as intense light, extremes of temperature, dessication, and erosion, that are sources of stress or mortality. The value of colonizing herbs in soil stabilization was demonstrated in the early part of the field tests, but the effect is not apparent in the results.

Species Removal

Several previous studies have examined the effects of species removal on the course of old-field succession. As with the seed and transplant plots of this study, research tends to support the view that succession cannot be succinctly explained by simple-concept models. In a field experiment designed to test whether annual plants were needed to "prepare the way" for perennial plants, McCormick (1968) removed annual plants from a portion of a first-year-old field in Pennsylvania but allowed them to grow elsewhere. The subsequent biomass of individual perennial plants on the annual-free areas was many (15 to 82) times greater than on

areas with annuals. Using the decision criteria of Connell and Slatyer (1977), this experiment supports the inhibition model.

Pinder (1974) studied the effects of the presence of the dominant grasses on the productivity of subordinate forbs within a perennial-grass, old-field community. He found that removing the dominants increased the net productivity of almost all subordinate species.

Hils and Vankat (1983) used the species-removal approach to test Connell and Slatyer's (1977) models in the first year of old-field succession. Their experimental treatments included removal of annuals, annuals and biennials, and perennials. Results from the first growing season favored acceptance of the initial floristics model, but the authors cautioned that more than one model of succession may apply in the same field at the same time, reflecting the spatial heterogeneity of the old-field community. The same old-field plots were further studied by Zimmerman and Vankat (1984). The species-removal treatments were maintained in the second year and the developing community was studied for the next three years. The initial floristics model was still supported at the end of 5 years because the authors found no statistically significant differences between the biomass of perennials grown with annuals and biennials and the biomass of those grown alone. Succession resulted in the development of nearly identical communities in the two treatments. The

two studies imply that the colonizing herbs had little effect on perennial herb species.

None of the four studies found any support for the relay floristics model, but all dealt with only herbaceous plants in an old-field succession sequence. As noted earlier, relay floristics may be most appropriate for describing primary succession and the establishment and growth of late successional woody plants.

The relay floristics model predicts that later successional woody species only enter the developmental cycle after harsh conditions have been ameliorated by the colonizing vegetation. The pioneer plant community is commonly assumed to play a role in the accumulation of soil organic matter, development of soil profiles, building of vegetation structure to provide shade and reduction of erosion from raindrops, buildup of soil nutrient levels, development of recycling from consumers, and development of symbiotic relations (plant/mycorrhizae, for example). Evidence in support of the relay floristics model comes from studies of primary succession on newly exposed surfaces. Crocker and Major (1955) and Lawrence et al. (1967) have suggested that the characteristics of soils newly exposed by a retreating Alaskan glacier make the establishment of plants extremely difficult. Pioneer species that are able to colonize will ameliorate these conditions, reducing pH, increasing nitrogen, adding a layer of organic matter over the hardpan, and reducing

desiccating winds. Seedlings of spruce trees appear under the new conditions, but seldom, if ever, on the original exposed sites. Another example is the primary succession on sand dunes on lake shores (Cowles, 1899; Olson, 1958). Pioneer plants stabilize the moving sand, which otherwise would be unsuitable for colonization by later-appearing species.

Competition

Three experimental treatments (enhanced legume, natural colonizers, and enhanced colonizers) provided three levels of examining the issue of relay floristics versus competition. The natural colonizer treatment looks at relay floristics in the classical sense. The enhanced colonizer treatment tests the hypothesis that "more is better" for the establishment of climax species. The enhanced legume treatment tests the role of nitrogen-fixing species as colonizers. Tall, fast-growing legumes like Sesbania macrocarpa, S. punicea, and S. vesicaria could provide shade for young seedlings, attract pollinators, and provide perches for birds and cover for small mammals. It was assumed all these benefits could accelerate the rate of ecosystem development.

With the exception of soil stabilization, none of these presumed benefits was as influential as the reduction in competition for resources during the first year of vegetation development at this particular site. It may be that scarce resources, such as moisture or soil nitrogen, limit vegetation

development and that the relatively slower-growing woody species show less vigorous growth when faced with herbaceous competitors. Because forest development is a long-term process (on the order of 50 to several hundred years), the experimental plots provide a very controlled view of only the earliest stages. It is possible that the presumed benefits of the early colonizers take time to occur and have an effect. The effect of litter may be an example.

Foresters have long noted competition as a factor influencing successful reforestation. Toumey and Korstian (1931) note that a low, dense cover of grasses and herbs is a decided disadvantage to reforestation; not only does it provide a retreat for rodents and other seed-eating animals but, as soon as germination occurs, it directly competes with the young seedlings. The roots of the herbaceous competitors draw nutrients and water from the surface layers of the soil, and the intensity of competition often proves fatal to the trees.

Competition has also been documented as a cause of decreased establishment and growth of tree seedlings in reclamation. Tackett and Graves (1983) cited competition by an herbaceous cover crop as a significant factor in reducing the height growth of tree seedlings. Vogel and Berg (1973) also found competition from herbaceous plants could be detrimental to growth of tree seedlings. Brown (1973) cited competition from herbaceous plants as one of the factors affecting germination and initial survival of seedlings.

Succession

The preceding discussion of the field test results effectively illustrates the uncertainties and contradictions impeding interpretation of ecosystem development. The three paradigms of succession (relay floristics, initial floristics, and inhibition) are too rigidly and narrowly constructed. The field tests used in this study, which followed the experimental design of Connell and Slatyer (1979), assume that the paradigms are mutually exclusive and that the pattern and course of succession is determined by only one. It is more likely that all three operate at some level during the course of succession. Hils and Vankat (1982) reached the same conclusion, finding that more than one model of succession may apply in one old-field at the same time reflecting the spatial heterogeneity of the old-field community.

Connell and Slatyer's (1977) approach appears to address only secondary succession. By omitting primary succession only implicitly, they further cloud the issue. As noted above, temporal factors need to be considered, and it is also likely that different paradigms may be appropriate at different stages of development.

Role of fauna in succession. The Connell and Slatyer (1977) approach is also deficient in not considering the role of micro- and macrofauna in ecosystem development. Animals serve such functions in the community as seed dispersal, and

pollination. This study addresses the effect of mound-building ants in ecosystem development on mined lands; the role of earthworms in soil turnover and nutrient cycling provides another well-documented example of the influence of animals on vegetation development.

Seed dispersal by animals, especially birds, is a potentially very important means for trees to invade disturbed areas. If the developing community provides the proper habitat requirements for seed-dispersing agents, then the invasion by later successional species may proceed much faster. Evidence of tree seed dispersal by birds can be seen in the woody flora found along almost any fence row, where seedlings of berry-producing species like black cherry (Prunus serotina), hercules-club (Zanthoxylum clava-herculis), and sugarberry are quite common. In many of the central Florida citrus groves abandoned after the severe winter freeze of 1983, laurel oak and black cherry seedlings invaded within the first year or two, typically found beneath the standing-dead citrus trees. This invasion pattern was a result of the perch sites provided by the dead citrus trees and used by the seed dispersing birds. Field studies by McClanahan (1984) and Wolf (1986) indicate that seed dispersal to a large degree determines the rate at which forested ecosystems recover from catastrophic disturbances such as strip-mining. For animal-dispersed seeds, site attractiveness appeared to be more important than distance.

Development of critical structure during primary succession. In primary succession on highly disturbed landscapes, the dispersal, arrival, and successful establishment of many late successional tree species may require some degree of "site preparation." The site attractiveness provides an excellent example of how seed dispersal is constrained until the site is suitable for the dispersal agent. Colonizing annuals, biennials, and herbaceous perennials do not offer attractive perch sites for many seed-dispersing birds.

Many tree species have obligate or facultative symbiotic relationships with soil fungi, called mycorrhizae. The successful establishment and growth of some late successional tree species may be tied to presence of the appropriate fungal symbiont (Wallace, 1988). The aboveground succession may be linked to a belowground succession.

Caveats

Finally, some degree of caution is needed in interpreting the first-year results from the Gardiner seed and seedling plots. Some of the most obvious considerations are as follows:

1. Results are from a single growing season but conclusions are extrapolated to the long-term process of ecosystem development.

2. Experimental treatments were fixed, not random; therefore, statistical inferences are appropriate only

to the treatment levels selected and not to a population of possible levels.

3. A limited number of tree species was used in the tests, and although the responses of the species differ, results are interpreted in terms of a whole forest.

4. Results are from a single set of tests carried out on one soil type at one site, so conclusions about the process of forest development must be couched in appropriate scope and scale.

6. Allelopathic effects of herbaceous species on each other and on woody plants may be important and were not investigated.

7. The weeding treatment may provide indirect benefits by disturbing the soil, increasing the rate of water infiltration by breaking up soil crusts commonly found on exposed overburden soils.

8. In the seeded plots it was easier to locate and measure seedlings in the seed plots receiving the weeding treatment. It is possible that some small seedlings were overlooked in the other treatment plots. So, then germination results would be biased in favor of the weeded treatment.

Mound-Building Ants

Mound Survey

The mound densities measured in the survey ranged from 560/ha to 2,100/ha on 1 to 5-year old sites. Kangas (1983) found ant mound density increased dramatically over the first 10 years on unreclaimed phosphate-mined land, from 2,000/ha at 1 year to over 8,000/ha at a 10-year old site.

Adams et al. (1978) estimated fire ant mound density in agricultural fields in Brunswick County, North Carolina, at 141 mature mounds per hectare. Baroni-Urbani and Kannowski

(1974) estimated the fire ant mound density of a Louisiana pasture at 96/ha. The relatively lower mound densities in these two studies may be a result of site-specific factors, but are more likely due to the authors' focus on large mature mounds.

Kangas (1983) also noted a general increase in size of ant nests with increasing site age up to a point and then a later decline. For example, few ants were seen on a 50-year-old site. This observation may indicate a change or succession in the ant fauna through time as the vegetation, light levels, food quality, and physical and chemical character of the soil profile change.

Ant Mound Roles

Soil development Mound building affects soil bulk density, particle size distribution, and the amount and distribution of pore space. The bulk density of soils from the 2-year old site showed mound values to be approximately 80 percent of the non-mound values, 1.19 g/cm^3 versus 1.74 g/cm^3. Wali and Kannowski (1975) measured the bulk density on mounds of seven species of ants on prairies in northeastern North Dakota and found the values to lie in a narrow range of 0.64 to 0.75 g/cm^3 in comparison to 1.15 g/cm^3 for non-mound prairie soil. Levan and Stone (1983) measured the bulk density of a black meadow ant (Formica fusca) mound as 0.51 g/cm^3.

A reduction in bulk density may make the soil a better rooting medium for established plants and possibly for germinating seeds, as soil aggregates will be broken down. Probably more important than absolute density differences is the effect of breaking the surface crust. This may be especially true on overburden soils, which tend to form very hard surface crusts, because of a higher clay content than native soils. Density changes are primarily a result of the movement of individual soil particles or grains, which increases pore space. Increased pore space can facilitate gas exchange, evaporation, and water infiltration.

Mound building breaks up the crust aggregate, thereby increasing the pore space in the surface horizon. Concomitant with the surface effects of mound building is the creation of an elaborate subsurface system of chambers and tunnels. Tunnel systems extend as much as a meter or more below the mound and lateral channels may extend outward from the mound typically for a distance of several meters. The extensive tunnel system creates an anastomosing network of interconnected soil macropores that is maintained for the life of the mound. Some of the soil profile alterations resulting from ant activities may be lost temporarily during intense rainfall, but the mound and tunnel system are quickly repaired by the colony.

Nest construction may cause more rapid alteration of the soil profile than would biogeochemical processes without

animals. Although mound construction is localized, a larger area affected is altered rapidly and extensively. Channelling below the mound produces an extensive interconnected network that penetrates the parent material. Deep channeling and vertical transport of soil material lead to an alteration of the soil.

Some of the changes may persist for some time after mound abandonment. The channel system gradually collapses and the mound slumps, but soil alterations and nutrient availability may selectively favor certain plant species long after the mound has been abandoned. Levan and Stone (1983) estimate that pedoturbation by ants can be quite significant when viewed over the long term. Assuming an average mound density of 2,000/ha and an average mound basal area of 25 cm mounds occupy approximately 5 percent of the landscape. If it can be further assumed that the average life of a mound is approximately 2 years (Lofgren et al., 1975), then all the soil in a given area may be affected in 40 years time.

Infiltration. An increase in infiltration rates beneficially alters the water balance of a developing community by preventing the loss of that scarce commodity, water. Water infiltration rates were higher in mound soils than non-mound soils in all measurements. The most obvious differences in the soil types were the pore space, texture, and bulk density.

Crusts commonly develop on the surface of overburden soils as they are alternately exposed to wetting and drying. The crust reduces infiltration and increases runoff relative to those areas where the crust has been broken. Crusting causes rainfall to pond on the soil surface, and blue-green algal mats commonly form on the most frequently ponded areas. Algal mats provide an additional barrier to water infiltration.

Ehlers (1975) found that earthworm burrows reaching the surface improve water drainage. Ursic and Esher (1988) demonstrated that small mammal burrowing significantly increased water detention-retention in a pine-covered catchment and concluded that the numerous interconnected surface and subsurface burrows created a system that could accept and retain rain water until it was transmitted to deeper layers or moved into the soil matrix. In simulated rain study plots with short-tailed shrews (Blarina carolinensis) and pine voles (Pitymys pinetorum), they showed that burrowing activities decreased surface runoff by approximately 25 percent.

Ant tunnels are soil macropores. Dixon (1971) concluded that large pores can have a profound effect on the infiltration of water into soils. In a model developed to study pore size in relation to infiltration, Edwards et al. (1979) demonstrated that surface-connected holes can

effectively transmit water when more water is applied than can infiltrate.

Nutrient cycling. Results of the chemical analyses support the hypothesis that foraging activity by ants elevates levels of some nutrients in the mound relative to adjacent non-mound areas. Confirmation of the nutrient concentration role of mound-building ants is one of the central points of a general model of the role of ants in ecosystem development (see Figures 4 and 5).

Fire ants have been extensively documented because of their status as nuisance pests. It is well established that fire ants are general landscape foragers with a diet consisting largely of protein from invertebrate prey supplemented with oils and fats from some plant parts (Lofgren et al., 1975). Foodstuffs are returned to the mound for consumption by the colony. The conceptual model predicts that because the ultimate fate of food materials is ant biomass and waste products, the mound should have relatively higher levels of organic matter and inorganic nutrients derived from microbial breakdown of organic matter in the mound. Soil chemical analyses showed enhanced nutrient pools in mounds and, therefore, support that pathway in the conceptual model.

Generally higher levels of exchangeable cations, particularly potassium, have been reported from ant mounds by Czerwinski et al. (1969, 1971), Gentry and Stiritz (1972),

Rogers and Levigne (1974), and Wall and Kannowski (1975). The statistically significant, higher levels of potassium mound soils are evidence of nutrient concentration by animals. Potassium may also come indirectly from phloem exudates via aphids (Levan and Stone, 1983), on which fire ants are known to feed (Lofgren et al., 1975).

Elevated sodium levels in mound soils are more perplexing. Sodium is a minor essential nutrient for animals but not for plants. It is also a readily solubilized ion from a variety of inorganic salts. It is possible that elevated levels of potassium and sodium may be the result of differences in evaporation rates between mound and non-mound soils. The lower bulk density and greater pore space of mound soils may facilitate evaporation of soil water, resulting in salt deposition. It is also possible that elevated levels of potassium and sodium in mound soils are caused by microbial decomposition of the organic matter in the mounds. The evaporation hypothesis remains one possible explanation of the elevated cation levels, but elevated organic matter and nitrogen levels provide additional support for the biological concentration argument.

Lack of statistically significant differences for calcium and magnesium is not surprising, as overburden soils containing limestone and dolomite typically have high concentrations of these cations. Concentrations of calcium and magnesium ranged from several hundred to several thousand

grams per kilogram in overburden soils (Wallace, 1988). The heterogenous nature of overburden soils led to considerable veriation among samples.

No clear differences in pH were observed between the two soil groups. Wali and Kannowski (1975) found ant activity increased pH in predominantly acid soils and decreased pH in predominantly alkaline soils. It is likely that there has not been sufficient time for ant activities to have an effect on the young overburden soils at the three sites studied. Also, the heterogenous nature of these soils may contribute to a large statistical variance. It is expected that a pH reduction attributable to activities of the colony will become apparent through time.

Plant growth enhancement. The results of the two plant growth experiments demonstrate that elevated nutrient levels in mound soil can translate into enhanced plant growth. The higher cations and nitrogen in mound soil enhanced growth for both a grass (*Paspalum urvillei*) and woody plant (*Liquidambar styraciflua*). This supports the field observation that herbaceous plants, especially grasses, growing on mounds were more robust than those on adjacent non-mound soils. Indirect evidance is also provided to support the existence of non-trophic feedbacks as shown in the feedback loop between plants and ants (see Figures 4 and 5).

Ant Model

The importance of mound-building ants in a developing ecosystem appears to lie in the capture and cycling of potentially scarce resources, such as nutrients and water. Growth and development can be stimulated in two ways: (1) by additions or supplements of energy or resources and (2) by concentrating and recycling existing resources at a faster rate. It is the latter method that ants appear to facilitate.

The results of the storages and pathways investigated support the ideas used to develop the conceptual ant model (see Figures 4 and 5). Mounds were found to have elevated nutrient levels that, in turn, produced enhanced plant growth in greenhouse studies. Taken together, these results support the existence of a positive feedback loop between ants and primary producers. The existence of the other proposed feedback, the effect of ant-mediated pedoturbation on primary producers, appears to be supported by the infiltration tests.

Indirect evidence of microbial pathways was found accumulations of organic matter and nutrients. Czerwinski et al. (1971) showed that enhanced organic matter levels in ant mounds increased activity of bacterial and fungal decomposers.

Physical soil alterations resulting from mound building were not directly linked to enhanced plant growth, but indirect evidence comes from the beneficial effects of

biologically mediated soil turnover on plant growth (Gentry and Stiritz, 1972; Platt, 1975).

The effects of ants in a developing post-mining landscape will not be limited to the role of fire ants, as other soil fauna with both similar and different life histories are also present on these sites. In addition, the composition of the soil faunal community will likely change through time.

Fire ants are an exotic species but do not appear to serve an exotic function. While they are able to displace other native species of ants, in their absence the native species can occupy these sites and serve the same function. Some other ant species may influence the developing ecosystem in similar ways at different stages.

It is expected that as the post-mining landscape matures, ants may decline in dominance while earthworms gradually become more important components of the soil microfauna. Ants and earthworms may perform much the same function at different stages of succession. The two intensify different stages of decomposition; ants mainly with the first stages of mineralization and earthworms with humification. Petal (1978) has argued that the contribution of these two groups of animals to processes within the ecosystem and the range of their influence are functionally equivalent in environments with different fertility, plant productivity, rate of decomposition, and trophic complexity. In infertile soils with low organic matter and decomposition rates, like young

overburden soils, ants speed the return to the soil of nutrients accumulated in the bodies of other animals. The role of earthworms appears to be greater in fertile soils, characteristic of more mature ecosystems, where they speed the release of nutrients from the organic matter as it is being decomposed.

Eclectic Synthesis of Paradigms and Implications for Reclamation Design

Evidence reported in this dissertation supports the conclusion that both allogenic and autogenic forces act to change vegetation during primary succession on reclaimed upland and wetland sites. An encompassing paradigm of ecological succession must recognize the action of both forces and the interplay or feedback between them. With regard to the competing paradigms (initial floristics, inhibition, relay floristics, coevolution, and self-organization), studies reported here indicate that all are operating either simultaneously or at some time during succession on mined lands. It is likely that different paradigms may be appropriate at different stages of ecosystem development.

There is no doubt that ecosystems can be studied either by examining one mechanism at a time or with a holistic, synthetic ecosystem approach and that valuable information is contributed by both approaches. It is premature to assert that a synthesis is not possible (Peet and Christiansen,

1980), but it is clear that the synthesis is far from complete. The continuing contradictions about succession after many decades of study suggest that ecology and the succession concept may be in the midst of a change in paradigm. The single concept paradigms of succession (inhibition, initial floristics, relay floristics in particular) appear to be flawed and a new paradigm will likely emerge from a more eclectic synthesis that incorporates and unifies the concepts of several paradigms. It is clear that an explanation of the cause and mechanism of succession, and development of a reasonable consensus on a paradigm of succession, will require a careful analysis of the historical background, biases and premises, and philosophy of the idea and its practitioners, critics, and proponents.

Until such time that a unifying paradigm of succession is constructed and widely accepted, it is also clear that the five competing paradigms examined in this dissertation can provide a theory-based guide for the reclamation of disturbed land. Reclamation should be viewed as type of engineering design based on ecological principles. The five paradigms reviewed in this dissertation can be used as ecological principles for guiding reclamation design. Using the paradigms to guide our reclamation design efforts should help us create functional, self-maintaining ecosystems that integrate with the surrounding landscape. A clear understanding of succession also provides an opportunity for

forming rational and cost-effective land reclamation techniques and policies that will enhance and direct the successional process on mined lands.

Using the five individual paradigms as design principles, some of the implications of each for the reclamation of strip mined land are discussed in the following section.

Inhibition

There are many documented examples of inhibited or arrested succession on mined lands. These studies generally describe an arrested succession in which the initial species composition of primary invading species is perpetuated. The Fort Green marsh study indicated that in the absence of disturbance, the initial vegetation pattern and species composition are maintained for some time, possibly even long-term.

Initially established vegetation may be able to resist invasion by other species through maximum performance for existing environmental conditions. Under appropriate conditions, even slow-dispersing, late successional species are able to become established and occupy the available space. Once the available space is filled, opportunity for invasion, even by aggressive species capable of inhibiting succession, is limited. Consequently, it is feasible to establish self-maintaining, stable, wetland and upland communities

dominated by late successional species able to resist invasion by aggressive colonizers.

The arrested, or inhibited, succession observed on mined lands may be largely attributable to restrictions on dispersal. It is apparent from the field studies reported here that late successional plant species can become established, grow, and survive under early successional conditions. The successional process on disturbed lands can be influenced and enhanced by facilitating the dispersal and establishment of the more slowly arriving, later successional components.

For reclamation, the emphasis should be on: (1) predicting the soil type and soil moisture conditions (hydroperiod in wetlands) of the reclaimed system and using these as guides for determining the type of vegetation that could be supported; (2) controlling aggressive species capable of inhibiting succession; and (3) overcoming the dispersal limitation of many late successional species to get these species established at the start. On wetland sites, the application of peat or muck from donor marshes has been successful in these areas but may not always be feasible because of the quality of donor material or budgetary constraints in transporting the material. In such situations, planting an array of long-lived perennials in patches can accomplish these goals. At Fort Green large stands of cattail, pickerelweed, and bulrush developed from individual

plants or patches that gradually coalesced into larger units. A patch has to be of some critical size before it can be successfully established, and that the "critical" patch size probably changes as a function of the surrounding vegetation, the amount of open space available, and the growth rate of the species. On upland sites, woody species characteristic of later successional stages can be easily planted or seeded during early revegetation efforts.

In some cases an arrested successional stage may be desireable, such as along utility line rights-of-way. If so, then revegetation efforts can be targeted at enhancing the establishment of those species capable of arresting succession on disturbed lands. The use of grazing, mowing, and periodic burning can also be helpful tools for arresting succession. For instance, fire may be needed for preventing the encroachment of woody species into marsh systems.

Initial Floristics

Egler's initial floristic hypothesis portrays old-field succession as a seed bank response to a change in environmental conditions. Studies in this dissertation show that initial floristics is also an important factor during primary succession on upland and wetland sites. The initial floristic composition is an important determinant of the type of vegetation that develops following disturbance. The vegetation pattern, and species composition of the marsh

community at Fort Green was found to be a function of the interplay between the propagules available and the prevailing environmental conditions.

The formation of a seed bank in created wetlands appears to be a relatively rapid process, beginning almost immediately after the land surface has been exposed, but the species present in the seed bank samples were predominantly the initial colonizing species. Notably absent were seeds of the late successional species: woody taxa, emergent macrophytes, submergent macrophytes, and free-floating aquatic species.

The implication of the initial floristics paradigm for reclamation design is that within certain constraints the species composition of reclaimed upland and wetland communities can be influenced, an in particular late successional species can often be established from the start. For wetland systems, design should focus on the seed/propagule bank as a critical component of self-maintaining systems. The use of peat or muck from donor wetlands can provide an instant seed bank that contains seeds/propagules of early and late successional species. As shown by the success of the bulrush plantings at Fort Green, some perennial macrophytes can be easily established by planting. A diverse array of woody species can be successfully established by seedling plantings in both wetland and upland situations.

Relay Floristics

In a few cases relay floristics has been demonstrated. The results from the Gardinier tree plots showed that during primary succession areas subject to erosion and/or unstable substrates require a cover crop or nurse crop of early successional species in order to stabilize the substrate before later successional species can become established. In most areas, natural colonization by rapidly dispersing species will typically provide a cover crop within the first growing season. In areas subject to erosion, reclamation efforts should enhance and accelerate establishment of a cover crop. Seeding is one commonly used method. Spreading of topsoil/muck from donor upland/wetland sites is another method.

Coevolution

Within the constraints of resource supply or other environmental factors the autogenic, biological system is characterized by strong positive feedbacks among its components. Classic mutualisms exist between plants and mycorrhizal fungi, pollinators, and seed dispersers to name a few examples, but there are also the extended mutualisms that exist between plants and their rhizosphere, as well as the interactions that may not fit the standard definition of mutualism at all, but nonetheless are characterized by strong

mutualism at all, but nonetheless are characterized by strong positive feedback among the system components. The fire ant model may be an example of this latter type of positive feedback relationship. Severe disturbances, such as strip-mining sever these links; re-establishing these links should be an important part of land reclamation.

As discussed earlier, the maturation process within a developing community largely results from autogenic processes. One implication of this for reclamation design is that mature ecosystems have accumulated structure, and in many cases some of this critical structure can be added during reclamation. The application of muck from a donor wetland provides not only a propagule bank of seeds and rhizomes but structure in the form of the organic material itself and its attendant microbial and microfaunal component. As noted in the studies reported in this dissertation, other kinds of autogenically produced structures can be critical to development of communities in a primary succession. Some of these critical structures can also be added to the reclaimed system. Specific plantings to augment food or cover, placement timber or brush piles to augment cover, or placement of structures to provide nesting and resting sites may improve site attractiveness for seed dispersing fauna on both upland and wetland sites. Implicit in the the use of these techniques is the assumption that they are cost-effective, that the cost of adding structure will be more than paid for in the benefits

derived. Further study and analysis will be required to make that determination, as the issue was not addressed in this dissertation.

In addition to seed dispersal, animals serve many other functions in the community such as pollination, nutrient cycling, and substrate turnover. The fire ant study demonstrated the beneficial effects of soil fauna on chemical and physical properties of overburden soils. Recovery of ecosystems after severe disturbance includes re-establishing the below-ground community and processes, and coupling the above-ground succession with the below-ground succession. Reclamation activities should encourage the formation of a diverse soil fauna. Factors likely to contribute to the return of a rich soil fauna which can be easily incorporated into a reclamation design include: (1) vegetation of high species richness, (2) a high plant cover, and (3) a widespread and thick litter layer over at least part of the area, and the presence of some logs and standing dead wood. For example, specific plantings can help with the first two items and trees, topsoil, litter and woody debris from the pre-mining land-clearing operations can be stockpiled and reused later to create litter patches, brush-piles and downed logs.

Self-Organization

In the self-organization paradigm, the actual species composition of the community is a function of the system's

self-organizing choices. It is believed that diversity stabilizes many ecosystem during environmental fluctuations or other periods of potential stress, buffering the system by providing more self-organizational choices, that extend the range of environments in which community structure and processes, such as energy flow, can be maintained.

Seed/propegule banks and accumulated below-ground structures (e.g., roots, rhizomes) provide a storage of "choices" for all environmental contingencies, providing some support for the self-organization paradigm. In wetland and upland communities, seed banks provide a mechanism for rapid recovery from catastrophic mortality resulting from fire, clear-cutting, and drought. The rapid response of seed banks to environmental change minimizes interruptions to the energy flow in the community helping to maximize overall primary production. A relatively continuous flow of energy through an ecosystem, even during recovery periods, prevents an uncoupling of the above-ground and below-ground components, since many rhizosphere processes depend upon energy inputs from the above-ground community.

It appears that many mature, self-maintaining wetland and upland systems contain a sufficient number of "choices" to meet a variety of environmental contingencies. Duplicating, or mimicking the "choices" found in many natural ecosystems by incorporating diversity into reclamation may prove to be a valuable design principle for creating self-maintaining

systems. The reclamation design principle then is to create wetland and upland systems that contain (1) a variety of habitat conditions with a variety of soil types and soil moisture conditions, and some variation in microtopography; (2) a diverse assemblage of plants with many representatives of all life history strategies; (3) habitat conditions needed to enhance the formation of a diverse soil fauna; and (4) habitat conditions needed to enhance the use of the site by a diverse assemblage of wildlife. Once the reclamation effort has provided a diverse array of choices, then the system can "choose" the actual species composition of the community.

CONCLUSIONS

The following points summarize the major conclusions relating to the wetland and upland field studies and their implications for reclamation and the paradigms of succession:

1. The application of muck from a donor wetland provides not only a propagule bank of seeds and rhizomes but structure in the form of the organic material itself and its attendant microbial and microfaunal component.
2. The development of the seed bank within the wetland, as seen by the spread of bulrush and Sagittaria, demonstrates the workings of an autogenic process and may provide one measure of community maturity. The spread of bulrush and Sagittaria also indicates that emergent macrophyte species other than cattail are capable of invading open mineral soils in reclaimed marshes.
3. The studies of wetland community development at Fort Grass show that the marsh communities resulting from the muck treatment had a different species composition than those arising by natural succession. These community differences also proved to be stable for the first four growing seasons.

4 Under appropriate conditions, even slow-dispersing marsh species are able to become established and occupy the available space. Once the available space is filled, opportunity for invasion, even by aggressive weedy species like cattail, is limited.

5 Marsh studies at the Fort Green site have shown the value of documenting specific site histories, beginning if possible with an unvegetated substrate. Long-term studies provide the best view of ecosystem development.

6 The Gleasonian model proposed by van der Valk (1981) appears to have merit as a partial descriptive paradigm of wetland species composition in secondary succession. It does not recognize the autogenic processes that can feedback to and influence the "environmental sieve."

7 Evidence was found in the upland tree seedling plots to support the operation of all paradigms: inhibition, initial floristics, relay floristics, coevolution, and self-organization. A unified paradigm that the ideas of all five paradigms will provide an eclectic resolution to the controversy.

8 Field studies show that mound-building ants can influence soil structure, runoff and soil infiltration, nutrient cycling, plant growth, and plant species distribution. Similar effects have been documented for the soil fauna in other ecosystems.

9 The arrested succession observed by many researchers on

mined lands may be largely attributable to restrictions on dispersal. Late successional plant species in marsh, swamp and upland ecosystems can become established, grow, and survive under early successional conditions. The successional process on disturbed lands can be influenced and enhanced by facilitating dispersal and adding the more slowly arriving components.

10. The upland forest seed plots show that good germination results can be obtained with direct seeding. Until recently, the industry has not had much success with getting seeds to germinate and survive. While direct seeding of woody plants has been shown to be feasible, it has not been demonstrated to be a cost-effective reclamation technique. Very small seedlings appear to be more vulnerable to stress and mortality than larger seedlings.

REFERENCES

Abaturov, B. D. 1972. The role of burrowing animals in the transport of mineral substances in the soil. Pedobiologia 12: 261-266.

Adams, C. T., J. K. Plumley, W. A. Banks, and C. S. Lofgren 1976. Impact of red imported fire ant, Solenopsis invicta Buren, (Hymenoptera, Formicidae), on harvest of soybeans in North Carolina. J. Elisha Mitchell Sci. 102:150-153.

Alvarado, A., C. W. Beriah, and F. Peralta. 1961. Leaf cutter ant (Atta cephalotes) influence on the Adepts in Costa Rica. Soil Sci. Soc. Amer. J. 45:790-794.

Atlavinyte, O., and J. Daciulyte. 1969. The effect of earthworms on the accumulation of vitamin B_{12} in soil. Pedobiologia 9:165-170.

Beroni-Urbani, C., and P. B. Kannowski. 1974. Patterns in the red imported fire ant settlement of a Louisiana pasture: some deaographic parameters, interspecific competition and food sharing. Env. Ent. 3:755-760

Baxter, F. F. and F. D. Hole. 1967. Ant (Formica cinerea) pedoturbation in a prairie soil. Soil Sci. Soc. Amer. Proc. 31.425-426.

Beattie, A. J., and D. C. Culver. 1981. The guild of myrmecochores in the herbaceous flora of West Virginia forests. Ecol. 62:107-115.

Beattie, A. J., and N. Lyons. 1975. Seed dispersal in Viola (Violaceae): adaptations and strategies. Amer. J. Bot. 62:714-722.

Berack, C. J. 1966. Conditions controlling wetland development on a phosphate mined reclamation site in Florida. M. S. Thesis. University of Florida, Gainesville.

Bertness, M. D. 1985. Fiddler crab regulation of Spartina alterniflora production on a New England salt marsh. Ecol. 66:1042-1055.

Bartrand, A. R. 1965. Rate of water intake in the field. In C.A. Black (ed.), Methods of Soil Analysis. American Society of Agronomy, Madison, Wisconsin.

Best, G.R., and K. Erwin. 1984. Effects of hydroperiod on survival and growth of tree seedlings in a phosphate surface-mined reclaimed wetland. In 1984 Symposium on Surface Mining, Hydrology, Sedimentology and Reclamation. Univ. of Kentucky, Lexington, Kentucky.

Bormann, F. H., and G. E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer Verleg, New York. 253 pp.

Bornemisza, G. F., and C. H. Williams. 1970. An effect of dung beetle activity on plant yield. Pedobiologia 10:1-7.

Brown, B. J. 1982. The role of herbivory in high and low diversity tropical agro-ecosystems. Ph.D. dissertation, University of Florida, Gainesville.

Brown, J. H. 1973. Site factors and seeding methods affecting germination and survival of tree species direct seeded or surface-mined areas. West Virginia University Agriculture Experimental Station Bulletin 620. 25 pp.

Bullock, S. H. 1974. Seed dispersal of Dendromecon by the seed predator Peromyscus. Madrono 22:378-379.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. J. Forestry 39:388-394.

Chew, R. M. 1974. Consumers as regulators of ecosystems: an alternative to energetics. Ohio J. Sci. 74:359-369.

Clements, F. E. 1916. Plant succession: An analysis of the development of vegetation. Publication No. 242. Carnegie Institution of Washington. Washington, D.C.

----------. 1920. Plant indicators. The Relation of Plant Communities to Process and Practice. Publication No. 290. Carnegie Institution of Washington. Washington, D.C.

Clewell, A. F. 1981. Vegetational restoration techniques on reclaimed phosphate strip mines in Florida. J. Soc. Wetland Sci. 1:158-170.

_____. 1983. Riverine forest restoration efforts on reclaimed mines at Brewster Phosphates, Central Florida. In D. J. Robertson (ed.), Symposium on Reclamation and the Phosphate Industry. Florida Institute of Phosphate Research, Bartow, Florida.

Connell, J. H. and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111:1119-1144.

Cowles, H. C. 1899. The ecological relations of the vegetation of the sand dunes of Lake Michigan. Bot. Gaz. 27:95-117.

Crane, D. 1972. Invisible Colleges: Diffusion of Knowledge in Scientific Communities. University of Chicago Press, Chicago. 425 pp.

Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecol. 43:427-448.

Culver, D. C., and A. J. Beattie. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado montane meadow. Ecol. 64:485-492.

Czerwinski, Z. 1971. The influence of ant hills on meadow soils. Pedobiologia 11.277-285.

Czerwinski, Z., H. Jakubczyk, and J. Petel. 1969. The influence of the ants of the genus Myrmica on the physico-chemical and microbiological properties of soil within the compass of ant hills in Staelackie meadows. Polish Journ. of Soil Science 3:51-58.

Dixon, A. F. G. 1971. The role of aphids in wood formation. I. The effect of the sycamore aphid, Drepanosiphum platanoides (Schr.) (Aphididae), on the growth of sycamore, Acer pseudoplatanus (L.). J. Appl. Ecol. 8:165-179.

Drury, W. H. and I. C. Nisbet. 1971. Interrelations between developmental models in geomorphology, plant ecology, and animal ecology. Gen. Syst. 16:57-68.

_____. 1973. Succession. J. Arnold Arboretum. 54:331-368.

Edwards, W. M., R. R. van der Ploeg, and W. Ehlers. 1979. A numerical study of noncapillary-sized pores upon infiltration. Soil Sci. Soc. Amer. Journ. 43:851-856.

Egler, F. E. 1954. Vegetation science concepts, IV Initial floristic composition, a factor in old field vegetation development. Vegetatio 4:412-417.

Ehlers, W. 1975. Observations on earthworm channels and infiltration on tilled and untilled loess soil. Soil Science 119:242-249.

Erwin, K. L., G.R. Best, W. J. Dunn, and P. M. Wallace. 1985 Marsh and forested wetland reclamation of a central Florida phosphate mine. J. Soc. Wetland Sci. 5:87-104.

Franklin, J. F., and M. A. Henstrom. 1981. Aspects of succession in the coniferous forest of the Pacific Northwest In D. C. West, H. H. Shugart, and D. B. Botkin (eds.), Forest Succession: Concepts and Application. Springer-Verlag, New York. 517 pp.

Gentry, J. B., and K. L. Stiritz. 1972. The role of Florida harvester ant Pogonomyrex badius in old field mineral nutrient relationships. Env. Entomol. 1:39-41.

Gleason, H. A. 1917. The structure and development of the plant association. Bull. Torrey Bot. Club 43:463-481.

_____. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53:7-26.

_____. 1939. The individualistic concept of the plant association. Am. Midl. Nat. 21:92-110.

Griffin, B. C., and N. C. Mullins. 1972. Coherent social groups in scientific change. Science 112:959-964

Grime, J. P. 1978. Plant strategies and vegetation processes. John Wiley and Sons, New York.

Grime, J. P. and R. Hunt. 1975. Relative growth rate: its range and adaptive significance in a local flora. J. Ecol. 63:393-422.

Nandel, S. 1976. Dispersal ecology of Carex pedunculata (Cyperaceae), a new North American cyraeccochora. Am. J. Bot. 63:1071-1079.

Heinselman, M. 1981. Fire and succession in the conifer forests of northern North America. In D. C. West, H. H. Shugart, and D. B. Botkin (eds.), Forest Succession: Concepts and Application. Springer-Verlag, New York. 517 pp.

Hils, M. H. and J. L. Van Kat. 1982. Species removals from a first-year old field plant community. Ecol. 63(3):705-711.

Hopp, H., and C. S. Slater. 1948. Influence of earthworms on soil productivity. Soil Sci. 66:421-428.

Horn, H. 1971. The adaptive geometry of trees. Monog. Pop. Biol. 3. Princeton Univ. Press, Princeton, New Jersey.

_____. 1974. The ecology of secondary succession. Ann. Rev. Ecol. Syst. 5:25-37.

_____. 1975. Forest succession. Sci. Am. 232(5):90-98.

Humphrey, S. R. 1979. Biological communities recovering after mining. Paper presented at the Reclamation of Surface-Mined Lands in the Southeastern Coastal Plains workshop, September 10-11, sponsored by the Center for Environmental and Natural Resource Programs, Institute of Food and Agricultural Sciences, University of Florida, Gainesville.

Hutchinson, G.E. 1942. Addendum to R. L. Lindeman. The trophic dynamic aspect of ecology. Ecol 23:417-418.

Johnson, E. A. 1975. Buried seed populations in the suberctic forest east of Great Slave Lake, Northwest Territories. Can. J. Bot. 53:2933-2941.

Kangas, P. 1979. Succession on spoil from phosphate mining. Center for Wetlands, University of Florida, Gainesville.

_____. 1983. Energy analysis of landforms, succession, and reclamation. Ph.D. Dissertation, University of Florida, Gainesville.

Keddy, P. A. and A. A. Reznicek. 1982. The role of seed banks in the persistence of Ontario's coastal plain flora. Amer. J. Bot. 69(1):13-22.

King, T. J. 1977. The plant ecology of ant-hills in calcareous grasslands: II. Succession on the mounds. J. Ecol. 65:257-278.

King, T. L., L. Hord, T. Gilbert, P. Montobano, and J. N. Allen, Jr. 1980. An evaluation of wetland habitat establishment and wildlife utilization in phosphate clay settling areas. IN R. R. Lewis and D. P. Cole (eds.), Seventh Annual Conference: The Restoration and Creation of Wetlands. Hillsborough Community College, Tampa, Florida.

Klawitter, R. A. 1959. Direct seeding hardwoods. In F. W. Woods (ed.), Direct Seeding in the South, 1959; Proceedings of symposium. Duke University, School of Forestry, Durham, North Caroline.

Kuhn, T. 1970. The Structure of Scientific Revolutions, 2nd ed. University of Chicago Press, Chicago. 233 pp.

Lawrence, D. B., R. E. Schoenike, A. Quispel, and G. Bond. 1967. The role of Dryas drummundii in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. J. Ecol. 55:793-813.

Leck, M. A. and K. J. Graveline. The seed bank of a freshwater tidal marsh. Amer. J. Bot. 66(5):1006-1015.

Lee, J. J., and D. L. Inman. 1975. The ecological role of consumers--an aggregated systems view. Ecol. 56:1455-1458.

Leven, M. A., and E. L. Stone. 1983. Soil modification by colonies of black meadow ants in a New York old field. Soil Sci. Soc. Amer. J. 47:1192-1195.

Lewis, R. R. III. 1982. Mangrove forests. In R. R. Lewis, III (ed.) Creation and Restoration of Coastal Plant Communities. CRC Press, Boca Raton, Florida.

Lofgren, C. S., W. A. Banks, and B. M. Glancey. 1975. Biology and control of imported fire ants. Ann. Rev. Entomol. 19.1-30.

Lugo, A.E., E. G. Farnworth, D. Pool, P. Jerez. 1973. The impact of the leaf cutter ant Atta colombica on the energy flow of a tropical wet forest. Ecol. 54:1292-1301.

Majer, J. D., J. S. Day, E. D. Kabay, and W. S. Farriman. 1984. Recolonization by ants in bauxite mines rehabilitated by a number of different methods J. Appl. Ecol. 21:355-375.

Marks, P. L. 1974. The role of pin cherry (Prunus pennsylvanica) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monog. 44(1):73-88.

May, J. T., C. L. Perke, and R. F. Perkins. 1973. Establishment of grasses and tree vegetation on spoil from kaolin clay strip mining. In R. J. Hutnik and G. Davis (eds.), Ecology and Reclamation of Devestated Land, vol. 2. Gordon and Breach, New York.

McClanahan, T. R. 1984. The effects of dispersal on ecological succession and optimal island size. M. S. Thesis. University of Florida, Gainesville.

McCormick, J. 1968. Succession. Via 1:1-18.

McIntosh, R. P. 1980. The relationship between succession and the recovery process in ecosystems. In J. Cairns (ed.), The Recovery Process in Damaged Ecosystems. Ann Arbor Sci. Pub., Ann Arbor, Michigan.

_____. 1981. Succession and ecological theory. In D. C. West, H. H. Shugart, and D. B. Botkin (eds.), Forest Succession:Concepts and Application. Springer-Verlag, New York.

McNaughton, S. J. 1979. Grazing as optimization process: grass-ungulate relationships in the Serengeti. Am. Nat 113:691-703.

Mitch, W. J., and J. G. Gosselink. 1986. Wetlands. Van Nostrand Rheinhold Co., New York. 537pp.

Myers, R. 1983. Unpublished seed bank data from Lake Kanapaha, Alachua County, Florida. University of Florida, Gainesville.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262-270.

Odum, H. T. 1983 Systems Ecology: An Introduction. John Wiley & Sons, New York.

_____. 1984. Summary: Cypress swamps and their regional role. In K. C. Ewel and H. T. Odum (eds.), Cypress Swamps. University Presses of Florida, Gainesville.

Odum, W. E. 1988. Predicting ecosystem development following creation and restoration of wetlands. In J. Zelazny and J.S. Feierabend (eds.), Increasing our Wetland Resources. Proceedings of Conference. National Wildlife Federation, Washington, D.C.

O'Dowd, D. J., and M. E. Hay. 1980. Mutualism between harvester ants and a desert ephemeral:seed escape from rodents. Ecol 81:531-540.

Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Bot Gaz. 119:125-170.

O'Neil, R. V. 1978. Ecosystem persistence and heterotrophic regulation. Ecol. 54:1244-1253.

Owen, D. F., and R. G. Weigert. 1976. Do consumers maximize plant fitness? Oikos 27:486-492.

Patten, B. C. 1975. Ecosystems as a coevolutionary unit: A theme for teaching systems ecology. In G. Innis (ed.), New Directions in the Analysis of Ecological Systems. Simulation Council Proc. Vol. 5, Society for Computer Simulation. La Jolla, California.

Pearsall, W. H. 1920. The aquatic vegetation of the English Lakes. J. Ecol. 8:163-201.

Peet, R. K., and N. L. Christiansen. 1980. Succession: a population process. Vegetatio 43:131-140.

Perkin Elmer Corporation. 1980. Analytical methods for the atomic absorption spectrophotometry. Perkin Elmer Corp., Norwalk, Connecticut. 569 pp.

Petal, J. 1978. The role of ant in ecosystems. In M. V. Brian (ed.), Production Ecology of Ants and Termites. Cambridge University Press, Cambridge, England.

Phillips, E. A. 1959. Methods of Vegetation Study. Henry Holt and Co., New York. 105 pp.

Pickett, S. T. A. 1976. Succession: An evolutionary interpretation. Am. Nat. 110:107-119.

Pinder, J. E. 1975. Effects of species removal on an old field plant community. Ecol. 56:747-751.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger mounds in tall-grass prairie. Ecol. Monog. 45:285-305.

Raup, H. M. 1957. Vegetational adjustments to the instability of site. pp. 36-48. In Proc 6th Technical Meeting, International Union for Conserving Nature and Natural Resources, Edinburgh, Scotland.

Rice, E. 1974. Allelopathy. Academic Press, New York, New York. 352 pp.

Roberts, J. T., and E. R. Heithaus. 1986. Ants rearrange the vertebrate-generated seed shadow of a neotropical fig tree. Ecol. 67:1046-1051.

_____ 1974. Foraging activities of the western harvester ant in the short grass plains ecosystem. Env. Entomol. 3:420-424.

Rogers, L. E., and R. J. Lavingne. 1974. Environmental effects of western harvester ants on the shortgrass plains ecosystem. Env. Entomol. 3:994-997.

Rusbton, S. T. 1983. Examples of natural wetland succession as a reclamation alternative. In D. J. Robertson (ed.), Symposium on Reclamation and the Phosphate Industry. Florida Institute of Phosphate Research, Bartow, Florida.

_____. 1988. Wetland reclamation by accelerating succession. Ph.D. Dissertation. University of Florida, Gainesville.

Salem, M. Z., and F. D. Hole. 1968. Ant (Formica exsectoides) pedoturbation in a forested soil. Soil Sci. Soc. Amer. Proc. 32:563-567.

Salt, G. W. 1979. A comment on the term emergent properties. Amer Nat. 11:13-18.

Schnoes, R. S., and S. R. Numphrey. 1987. Terrestrial plant and wildlife communities on phosphate-mined lands in central Florida. Bulletin of the Florida State Museum 30:53-116.

Shrikhande, J. G., and A. N. Pathak. 1968. Earthworms and insects in relation to soil fertility. Curr. Sci. 17:327-328.

Shuey, A. G., and L. J. Swenson, Jr. 1979. Creation of freshwater marshes in west-central Florida. In D. P. Cole (ed.), Sixth Annual Conference: Restoration and Creation of Wetlands. Hillsborough Community College, Tampa, Florida.

Smith, R. L. 1980. Ecology and Field Biology. Harper & Row Publishers, New York. 835 pp.

Tackett, E. M. and D. H. Graves. 1983. Evaluation of direct-seeding of tree species on surface mines spoil after years. In D. H. Graves, and R. W. DeVore (eds.), Proceedings of 1983 symposium on Surface Mining, Hydrology, Sedimentology, and Reclamation. University of Kentucky, Lexington, Kentucky.

Thorpe, J. 1949. Effect of certain animals that live in soils. Sci. Monthly. 68:180-191.

Toumey, J. W. and C. F. Korstian. 1942. Seeding and planting in the practice of forestry. John Wiley and Sons, New York.

Ursic, S. J., and R. J. Esher. 1988. The influence of small mammals on stormflow responses of pine-covered catchments. Water Res. Bull. 24:133-139.

Ulanowicz, R. E., and W. M. Kemp. 1979. Toward canonical trophic aggregations. Am. Nat. 114:871-883.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecol. 62(3):688-696.

van der Valk, A. G. and C. B. Davis. 1978. The seed banks of prairie glacial marshes. Can. J. Bot. 54:1832-1838.

_____. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecol. 59(2):322-335.

Vogel, W. G. and W. A. Berg. 1973. Fertilizer and herbaceous cover influence establishment of direct-seeded black locust on coal-mine spoils. In R. J. Hutnik and G. Davie (eds.), Ecology and Reclamation of Devastated Lands, vol. 2. Gordon and Breach, New York.

Wade, D., J. Ewel, and R. Hofstetter. 1980. Fire in South Florida Ecosystems. U. S. Dep. Agric., Forest Service General Technical Report SE-17 125 pp. Southeast. For. Exp. Stn. Ashville, North Carolina.

Wadsworth, G. A. 1983. The development of techniques for the use of trees in the reclamation of phosphate lands: A project overview. In D. J. Robertson (ed.), Symposium on Reclamation and the Phosphate Industry. Florida Institute of Phosphate Research, Bartow, Florida.

Wali, M. K., and P. S. Kannowski. 1975. Prairie ant mound ecology: interrelationships of microclimate, soils and vegetation. In M. K. Wali (ed.) Prairie: A Multiple View. University of North Dakota Press, Grand Forks, North Dakota

Wallace, P. M. 1988. The role of mycorrhizae in reclamation of phosphate mined lands by ecological successional processes. M.S. Thesis. University of Florida, Gainesville.

Wallace, P. M., and G. R. Best. 1983. Enhancing ecological succession: 6. succession of endomycorrhizal fungi on phosphate strip mined lands. In 1983 National Symposium on Surface Mining, Hydrology, Sedimentology, and Reclamation. University of Kentucky, Lexington, Kentucky.

Webster, J. R., J. B. Wade, and B. C. Patten. 1974. Nutrient cycling and the stability of ecosystems. pp 1-27 In P.G. Howell, J. B. Gentry, and M. H. Smith (eds), Mineral Cycling in Southeastern Ecosystems. CONF-740513. NTIS, Springfield, Virginia.

Weller, M. W. 1981. Freshwater Marshes. University of Minnesota Press, Minneapolis, Minnesota. 146pp.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. 45:229-299.

Whittaker, R. H. 1953. A consideration of climax theory. Ecol Monog 23:41-78.

Wiken, E. B., K. Broerems, L. M. Lavkulich, and L. Farstad 1976. Biosynthetic alteration in a British Columbia soil by ants (Formica fusca Linne). Soil Sci. Soc. Amer. Proc. 40:422-426.

Wilson, U. S. 1980. The Natural Selection of Populations and Communities. Benjamin Cummings, Menlo Park, California. 186 pp.

Wilson, N. L., J. H. Collier, and G. P. Markin. 1971. Foraging territories of imported fire ants. Ann. Entomol. Soc. Amer. 64:660-665.

Witkamp, M. 1971. Soils as components of ecosystems. Ann. Rev. Ecol. Syst. 2:85-110.

Wolf, R. W. 1986. Seed dispersal and wetland restoration. M.S. Thesis. University of Florida, Gainesville.

Zellars-Williams and Conservation Consultants. 1980. Evaluation of pre-July 1, 1975 disturbed phosphate lands. Florida Department of Natural Resources, Tallahassee, Florida. 107pp.

Zimmerman, D. M. and J. L. VanKat. 1984. Effects of species removals on an old field community: A five-year examination of successional mechanisms. Bull. Ecol. Soc. Am. 65(2):65.

BIOGRAPHICAL SKETCH

Mr. Dunn was born on January 23, 1954, in Summit, New Jersey. After completing elementary and secondary education in New Providence, New Jersey, he entered Tufts University in 1972, where he majored in biology and received the Bachelor of Science degree in May 1976. From May 1976 through September 1977, he was employed as an herbarium assistant in the Phippen-Lacroix Herbarium at Tufts University. His graduate training began at the University of Florida in the fall of 1977. He took a leave of absence from his graduate studies to work in environmental consulting in 1979 and 1980, then returned to complete the requirements for the degree of Master of Science in botany in 1981. In 1981, Mr. Dunn entered the Environmental Engineering Sciences Department at the University of Florida as a doctoral candidate. In the fall of 1985, he joined Environmental Services and Permitting, Inc., as a senior scientist. He moved to the environmental consulting firm of CH2M HILL in 1986 and currently works as an environmental scientist with project management responsibilities in the areas of tertiary wastewater treatment using wetlands, water quality investigations, and general water resources issues.

He is married to Elizabeth Bondy. They have two handsome sons, Charlie and Sam.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

G. Ronnie Best, Chairman
Associate Research
Scientist,
Environmental Engineering
Sciences

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Howard T. Odum
Graduate Research
Professor,
Environmental Engineering
Sciences

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Clay L. Montague
Associate Professor,
Environmental Engineering
Sciences

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Stephen R. Humphrey
Professor,
Forest Resources and
Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Warren Viessman
Professor,
Environmental Engineering
Sciences

This dissertation was submitted to the Graduate Faculty of the College of Engineering and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy

May, 1989

Hubert A. Benes
Dean, College of Engineering

Dean, Graduate School